Master Patrimoine Naturel et Biodiversité

Université de Rennes

MASTER 2 PNB

year 2025-2026

INTERNSHIP REPORT OF :

MENARD CYANN

Dansk Ornitologisk Forening

BirdLife DANMARK

GEDSER FUGLESTATION

Migration intensity at a bottleneck : the temporal impact of weather on Eiders (*Somateria mollissima*) migration

Field drawing of Eiders roosting by Gedser point. ©Cyann Ménard

HOST ORGANISATION : BirdLife Denmark/Dansk Ornitologisk Forening

Training supervisor : ELLEY Tina, Manager of Gedser Bird Observatory

Anne Marie Cortesero, Sébastien Dugravot and Frédéric Ysnel

Co-heads of PNB Master's programme

AKNOWLEDGEMENTS

First, a really special thank you to Gabriel Caucal, who has been encouraging me on my journey into migration monitoring ever since we first met, and who provided me with valuable contacts to help me carry out the project I had in mind for this Master's thesis. I wouldn't have lived the same past months without your help.

Then, the warmest thanks obviously goes to my supervisor Tina, who believed in me and in this project from the beginning. You gave me the opportunity to conclude this master degree by working on my favourite topic, in a wonderful place. Thanks to you, I experienced migration monitoring as a responsible counter for the first (and definitely not the last!) time in my professional life. Thank you for your kindness, your guidance, our slightly messy meetings due to our overworking minds, and your great cakes.

Thanks Louis and Andreas for your advices and your feedbacks. You both taught me a lot, in the perfect continuation of what I have learnt for the past years.

Thank you Ole for the good company, in both sunny days and rainy mornings. I learnt a lot by your side at the point, and you helped me build the self confidence I needed to carry the counting alone.

Thanks to all the people I met at the station : Henrik, Annemarie, Mads, Anne, Søren, Hans, Vagn, Alba, Olga, Joakim, Olivia, Martina, Lua, Marek, Hannah. Thank you all for your passion and your company, you are the heart of the station. Some special thanks to people who are not in this list yet. To Sjoerd, for having the sweetest soul I have ever seen. Thank you for being such a kind roommate, and for always finding the prettiest rocks of the beach. To Mathilde, thank you for your friendship, our push-ups session, and our never ending chats. To Théophile, thank you for your passion, your enthusiast, your silliness, and of course for the French touch. To Mathilde and Storm, thank you for your kindness, your support and your words of encouragement. The last month wouldn't have been quite the same without your presence by my sides. Thank all of you for the great laughs, and the great moments.

An obvious thank you to my family, who have always been so supportive, even (and especially) from afar. Thank you also to my friends, for being such an essential part of my life. A special thank you to all the friends migration monitoring brought to me, for being such a caring and supportive community.

Eventually, thanks to all the people I have met during those past two years. I can't wait to see what life looks like on the other side.

And obviously, a special shout out to the birds, from France, Denmark, and elsewhere.

Tak for alt.

RESUME

Au cours de leur migration, les oiseaux migrateurs adaptent leur comportement en fonction de multiples facteurs parmi lesquels les conditions météorologiques jouent un rôle prépondérant. Ces conditions présentent des variations spatiales et temporelles qu'un individu migrateur doit intégrer dans les prises de décisions relatives à son comportement migratoire. À partir de données issues de dix années de suivi de la migration postnuptiale au sud du Danemark, cette étude vise à évaluer l'impact de la météo sur la migration d'une population d'Eider à duvet (*Somateria mollissima*). Les objectifs de cette étude sont de 1) évaluer comment la prise en compte des conditions météorologiques rencontrées par les individus en cours de route améliore l'analyse des mouvements migratoires ; 2) déterminer quand et comment les paramètres météorologiques influencent ces effectifs. Les données météorologiques ont été collectées le long des côtes suédoises à intervalles réguliers afin de représenter le trajet migratoire des Eiders. Une comparaison de modèles a montré que la prise en compte des conditions météorologiques le long du trajet migratoire explique mieux l'intensité migratoire que les seules conditions météorologiques locales. Les mouvements migratoires des Eiders sont favorisés par les vents d'ouest rencontrés quatre jours et deux jours en amont du site d'observation, ainsi que par une hausse des températures trois jours en amont, et par les vents forts la veille du comptage. Des conditions météorologiques locales défavorables, caractérisées par une hausse des précipitations et de forts vents de face, sont corrélées à une diminution du nombre d'individus. Cette étude souligne l'importance des conditions météorologiques rencontrées en cours de route sur les comportements migratoires, qui ne peuvent donc pas être interprétés uniquement depuis l'échelle du site d'observation. L'amélioration de nos connaissances sur les espèces migratrices en mer Baltique contribue à une meilleure compréhension des défis environnementaux auxquels ces oiseaux sont confrontés et de la manière dont ils pourraient être affectés par les modifications globales de leur environnement.

Mots-clefs : migration, Eider à duvet, mer Baltique, goulet d'étranglement, conditions météos

ABSTRACT

Migration is an important part of birds life cycle. Migrants adapt their behaviour according to many factors, among which weather plays a paramount role. Considering continuous spatial and temporal variations of weather conditions, each migrating individual will decide whether to initiate, continue, or stop their migration. Using 10 years of post-breeding migration data collected from a bottleneck migration monitoring place at the Southernmost point of Denmark, this study aims to assess the impact of weather on the migration of a sea duck, the common Eider (*Somateria mollissima*). The objectives of this study are 1) to assess the relative importance of *en route* weather compared to local ones on daily observations of Eiders; 2) to investigate how and when weather parameters impact those numbers. Weather data were collected at predefined lags of one day each along the Swedish coastline to represent Eiders' migratory path. Based on a model comparison, using both local and lagged weather was found explaining daily migration intensity better than local weather conditions alone. No effect of weather was found at a five-day lag scale. Wind direction has a positive effect on migration at both four-day and two-day lags. Temperature has a positive effect at three-day lag only. Adverse local weather conditions, characterized by precipitations and strong headwinds are correlated to a decrease in the number of individuals. This study highlights the importance of weather experienced *en route* on migratory behaviours, which cannot be interpreted from a local perspective only. Bottlenecks are relevant places to conduct studies about bird migration ecology, making the continuation of sampling effort in these locations essential. Improving our knowledge about species that migrate along the Baltic/Wadden Sea migration flyway contributes to a better understanding of the environmental challenges these birds face and how they might be impacted by global modifications in their environment.

Keywords : bird migration, common Eider, Baltic sea, bottleneck, weather conditions

TABLE OF CONTENTS

INTRODUCTION

The seasonal movements back and forth between reproductive and non-reproductive grounds, known as migration, are an essential part of the life cycle of many bird species (Alerstam, 1993; Newton, 2008). Far more than just a transit period, this behaviour allows them to track environmental variations across the globe (Flack *et al.*, 2022) and hence optimize their biogeographical use all year long (Winger *et al.*, 2025) with significant implications for reproduction (Clements *et al.*, 2022; Kokko, 1999), survival (Buechley *et al.*, 2021; Dillenseger *et al.*, 2026; Newton, 2025) and overall fitness of the migrating individuals due to carry-over effect (Clements *et al.*, 2022; Harrison *et al.*, 2011). Consequently, events and factors affecting an individual's migratory behaviour can lead to dramatic consequences at both population and species level (Inger *et al.*, 2010; Norris, 2005; Visser & Both, 2005).

Just like many other behaviours, migration and its different aspects are driven and influenced by a complex set of factors. These factors include intrinsic information, such as hormones and internal clocks impacting migration onset (Åkesson & Helm, 2020; Jacobs & Wingfield, 2000; Ramenofsky, 2011), body conditions (Alerstam & Lindström, 1990; Ożarowska & Meissner, 2024) or experience and social clues (Jarjour *et al.*, 2017; Jia *et al.*, 2024; Kjellén, 1992). However, migrants also use environmental clues such as landscapes constraints (Åkesson & Hedenström, 2007), vegetation green up (Amaral *et al.*, 2025; Amélineau *et al.*, 2021; Cerro *et al.*, 2025) and overall food resource availability (Berthold, 2001) to flexibly adjust their migration onset, phenology or in-flight behaviour. Among these factors, it is widely admitted that weather and climate conditions play a prominent role in migration characteristics (Shamoun-Baranes *et al.*, 2010).

Climatic and meteorological conditions influence every stage of the migratory journey, from the date of departure (King *et al.*, 2022; Shamoun-Baranes *et al.*, 2006; Xu & Si, 2019) to the synchronisation of arrival dates (Mayor *et al.*, 2017), including routes taken (Eisaguirre *et al.*, 2018; Shamoun-Baranes *et al.*, 2017; Vansteelant *et al.*, 2014), in-flight behaviour (Senner *et al.*, 2018), stop-over use (Dänhardt & Lindström, 2001; Kassara *et al.*, 2025; Klinner *et al.*, 2020) and migration duration (Shamoun-Baranes *et al.*, 2010) during both pre-breeding and post-breeding migrations.

Considering the important spatial and temporal variations in climatic and meteorological parameters (Seinfeld & Pandis, 2016), migratory individuals must constantly adapt to changing conditions. Integrating both intrinsic and environmental information, migrants consequently make continuous choices that can have paramount consequences for the rest of their migratory journey (Alerstam, 2011) and thus potentially decisive for every other aspect of their life cycle.

This decisional process, known as *en route decision making*, will initiate, maintain or stop one's migratory movement in response to the conditions experienced along the way (Åkesson & Hedenström, 2007; Jenni & Schaub, 2003). As individuals migrating during the same time-windows supposedly face relatively similar conditions, these decision-making processes can result in group movements and concentrated flows along the flyways (Aurbach *et al.*, 2020; Hüppop & Hüppop, 2011; Rüppel *et al.*, 2023).

Following the main migratory pathways, some areas can accentuate the condensed aspect of the migratory flow, with sometimes millions of individuals from different populations and different species travelling by at nearly the same time (Aurbach *et al.*, 2020; Cardenas-Ortiz *et al.*, 2020). These locations, known as bottlenecks, are mostly caused by the presence of geographical barriers funnelling the migration path. Conducting studies at such locations can help improving knowledge onto the migratory behaviour and ecology of species that could otherwise be difficult to observe or study (Wehrmann *et al.*, 2019). The study of the flows observed at bottlenecks can provide insight into the choices made regarding the route to take (Buechley *et al.*, 2018), as well as the conducive conditions that triggered migratory movements upstream of the bottleneck and led to intensification of the bird flow (Shamoun-Baranes *et al.*, 2010). Therefore, they can be particularly relevant for studying migration and have been widely used in that regard (e.g. Filippi-Codaccioni *et al.*, 2010; Martín *et al.*, 2016; Panuccio *et al.*, 2017).

Albeit some studies have indeed provided insights into the impact of environmental conditions, and especially weather, on the behaviour of individuals passing through these bottlenecks (Becciu *et al.*, 2023; Benjumea *et al.*, 2024; Miller *et al.*, 2016), the focus is still very often on the impact of local weather conditions on the detection and behaviour of individuals (Morales-Góngora *et al.*, 2025; Vansteelant *et al.*, 2014). Much less attention has been paid to whether migration intensity observed at bottlenecks reflects weather experienced earlier along the migration route. How migrants respond to weather conditions during their journey has been studied using embedded technologies such as GPS tracking (Buechley *et al.*, 2018), but these methods limit the number of individuals from whom information can be collected (Lindberg & Walker, 2007). The concentration of species and individuals sighted at bottlenecks can be a real asset for collecting large amount of data. Thus, conducting studies at such locations can be highly relevant to investigate the impact of en-route weather conditions on migratory behaviour without resorting to telemetry, especially with populations whose migratory route is already known.

Common Eiders (*Somateria mollissima*), hereafter Eiders, are large sea ducks whose range is concentrated in the Northern Hemisphere (BirdLife International, 2018). Of the existing populations, the Baltic/Wadden Seas flyway one is found mainly in the geographical area of the Baltic Sea (HELCOM Red List, 2024). Due to this restricted range, their breeding and wintering grounds, as well as their main migratory path, are well known. From late May to early September, this population breeds in the Gulf of Bothnia, the Gulf of Finland, and along the Swedish coast, before migrating towards their wintering grounds along the Danish or German coasts, in the Kattegat or the Wadden Sea (Borkenhagen, 2020; HELCOM Red List, 2024) (Figure 1.A).

The historical presence and significance of this population for local communities (Christensen, 2008) has led to the implementation of numerous studies and monitoring programmes (HELCOM Red List, 2024; Laursen, 1989). These studies have led to a better understanding of the range (Borkenhagen, 2020), breeding and wintering ecology (Laursen *et al.*, 2019; Morelli *et al.*, 2021), population trends (Desholm *et al.*, 2002; Ekroos *et al.*, 2012) as well as the threats (Christensen, 2008; Larsson *et al.*, 2014; Tjørnløv *et al.*, 2019) to this population. However, apart from the monitoring of this population for more than 30 years from several migration monitoring sites on both sides of the Baltic Sea (Trektellen, 2026a), the migration period remains largely understudied. Few studies address Eiders' migration ecology, sometimes under the scope of the impact of weather conditions on their migratory behaviour (Day *et al.*, 2000, 2004; Hanssen *et al.*, 2016) but surprisingly, this aspect has never been studied in the Baltic Sea population.

Understanding the spatial and temporal influence of weather on migrants decision-making process is key to understand migration ecology as a whole. In this prospect, the objective of this study is to assess when, and by what weather parameters the post-breeding migration movements of Eiders are triggered.

The primary aim of this study is to evaluate the relative importance of local and lagged-up weather conditions recorded along the migration route on the intensity of Eider post-breeding migration observed at a Baltic bottleneck. As weather variations may trigger or inhibit upstream migration movements (Rüppel *et al.*, 2023; Shamoun-Baranes *et al.*, 2017), it will supposedly have an impact on the number of individuals observed with a delay. Hence, it is assumed that including both local weather and lagged weather from likely up-route areas will explain daily migration intensity better than by using local weather only.

Taking in account the results of this primary analysis, we then aim to assess the impact of meteorological factors on said observed migration movements. It is expected that fewer individuals would migrate with high air temperature (Guillemette *et al.*, 2016, 2017), heavy rain and strong headwind (Delfino, 2024; Werfeli *et al.*, 2022), while favourable air conditions such as weak winds and tailwinds would have a positive impact on the number of individuals migrating (Dänhardt & Lindström, 2001).

METHODS

Study site

Located at the most Southern point of Denmark (GPS : 54°33'32.9"N ; 11°58'11.4"E), Gedser point was noticed as a relevant bird migration monitoring place since the 1970's (Lind, 2010), leading afterwards to the creation of Gedser Bird Observatory in 2001.

Originally established as a ringing station focusing on passerine migration between Scandinavia and wintering areas in Europe and Africa, the site has also proven to be particularly suitable for studying waterbird migration, among which the Eiders (*Somateria mollissima*). Eiders populations breeding in the Baltic sea find their wintering resources along the German and Danish coasts. As Eiders migrate mainly along the coasts, the waters between Gedser (Denmark) and Rostock (Germany) will act as a natural bottleneck funnelling them close by Gedser point during their post-breeding migration (Figure 1.B.).

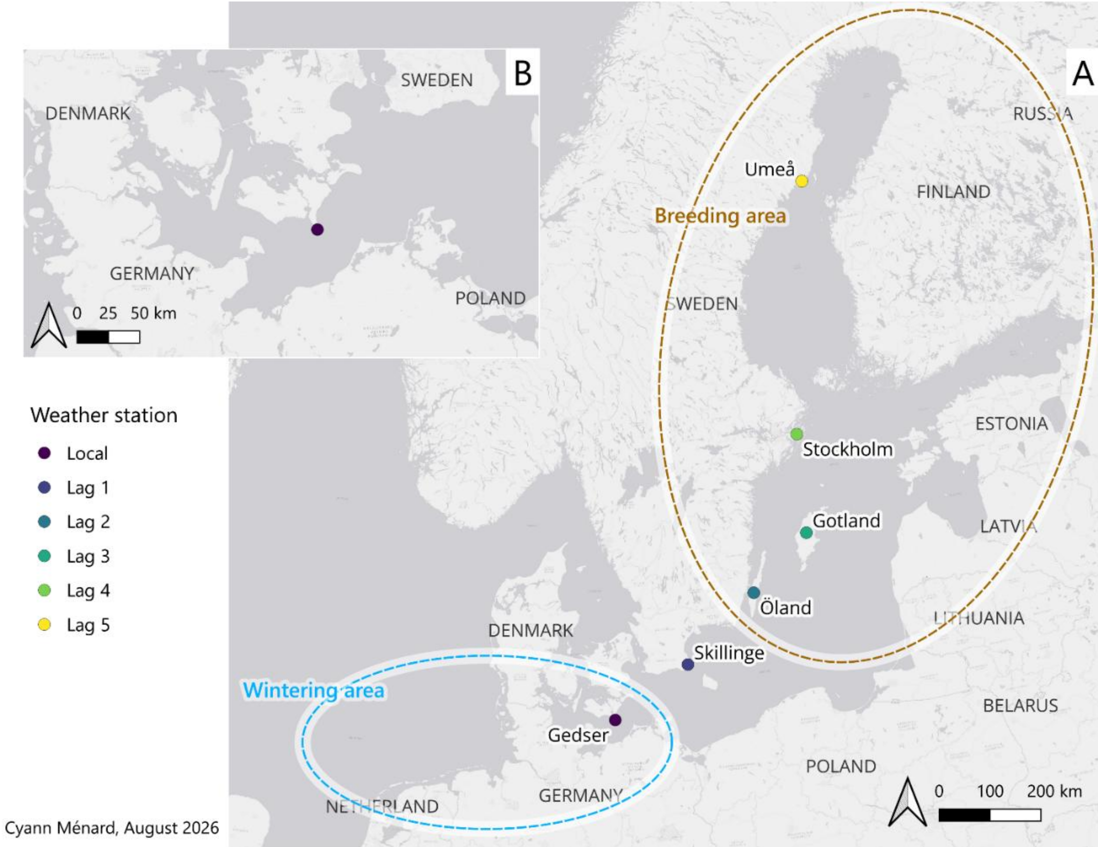


Figure 1 : A) Location of meteorological stations along the migratory path of the Baltic/ Wadden Sea flyway Eider population. Each lag has its own colour, from the darkest (Local weather at Gedser) to the lightest (5 days lag at Umeå). The breeding and wintering areas are also shown (respectively in brown and in blue). B) Visual representation of the bottleneck effect between Denmark and Germany. Gedser is the dark spot.

Data collection

In order to monitor Eiders' post-breeding migration, daily counts have been carried out from the 10th of August to the 20th of December, every year since 2004. To ensure comparable observation effort among years, the protocol became standardised in 2016 with a duration of 5 hours of counting, starting half an hour before sunrise. Therefore, only data collected between 2016 and 2025 are included in this analysis. In case of poor weather conditions, such as heavy rain, strong winds or extremely cold temperatures, as determined by the person responsible for the monitoring, the counting can either be cancelled, shortened or delayed when the conditions get better. Migration monitoring is conducted from Gedser headland (54°33'32.9"N ; 11°58'11.4"E), from where every migrating bird spotted through binoculars or with the naked eye is identified and counted. Additional information regarding the migration direction, the age and the gender of the individuals are also noted. The total numbers are then implemented in the Dansk Ornitologisk Forening (DOF) database (DOF, 2026).

After downloading all observations recorded at Gedser point by Gedser Bird Observatory between 2016 and 2025 from DOF database, only relevant data from post-breeding migration counts are kept for further analysis. To ensure consistent observation effort and avoid introducing additional sources of variation unrelated to the study objectives, only days with a complete standardised five-hour count in the morning were retained for analysis. In case of gaps in the data retrieved from DOFbasen, the missing days were collected on Trektellen (Trektellen, 2026b). As this study focuses on post-breeding migration, during which the birds are expected to migrate to their wintering grounds South-West of Gedser, individuals flying in directions other than South, South-West or West were excluded from the analysis. Total numbers of male, female or unsexed individuals were eventually added together to obtain the total number of migrating Eiders for each standard day of the study period.

Weather data

Both local and lagged weather information come from national meteorological institutes : the Danish Meteorological Institute (DMI), and the Swedish Meteorological and Hydrological Institute (SMHI). Local weather data comes from Gedser meteorological station (Figure 1.A, Table 1) and was downloaded through the DMI QGIS plugin (DMI Open Data *version 1.0.9*, (DMI, 2026) used on QGIS *version 3.44.8-Solothurn* (QGIS, 2026)). Lagged weather data comes from meteorological stations along the Swedish coast (Figure 1.A, Table 1) and were downloaded from the SMHI website (SMHI, 2026).

Weather stations were selected along the Swedish Baltic coast to represent weather conditions experienced by Eiders during the days preceding their arrival at Gedser. The selection was based on published information on migration routes and typical daily travel distances reported for migrating Eiders. Published estimates indicate daily travel distances of approximately 165–425 km, with typical movements around 200 km per day (Day *et al.*, 2004; Hanssen *et al.*, 2016; Mosbech *et al.*, 2006). Stations were chosen to approximate weather conditions experienced one to five days before arrival at Gedser (Figure 1.A), thereby allowing the influence of lagged weather conditions on migration intensity to be evaluated.

Table 1 : Meteorological stations information.

Temporal Lag	Location	Station name	Source	Altitude (above sea level)	Latitude (in decimal degrees)	Longitude
Local	Gedser	Gedser	DMI	3.26 m	54.5687	11.9435
One-day lag	Skillinge	Skillinge A	SMHI	4.02 m	55.489	14.3144
Two-day lag	Öland	Ölands södra udde A	SMHI	1.53 m	56.1977	16.4005
Three-day lag	Gotland	Fårösund Ar A	SMHI	12.76 m	57.9165	18.9533
Four-day lag	Stockholm	Svenska Högarna A	SMHI	11.81 m	59.4423	19.5022
Five-day lag	Umeå	Holmön A	SMHI	6.54 m	63.807	20.8645

For each station, the weather parameters of interest are the wind speed and direction, the temperature and the precipitation, each on a daily resolution (Table 2). For those parameters that were not available on a daily resolution, aggregate statistics were used to obtain either a daily average (Temperature, Precipitation, Wind speed) or the daily median (Wind direction). The median, rather than the average, was used for this parameter in order to better represent the typical weather conditions experienced by migrating Eiders during their day-to-day movements.

Table 2 : Weather parameters information

Parameter	Description	Unit	Source	Collection method (as reported by the organisations)	Daily aggregation method
Temperature	Air temperature	Celsius (°C)	DMI	daily average	Average
			SMHI	instantaneous value, once per hour, measured 2,0 m above ground level	
Wind direction	Direction from which the wind blows	Degree (°)	DMI	10-minute average, measured 10,00 meters above ground level	Median
			SMHI	10-minute average, once per hour, measured 10,0 m above ground level	
Wind speed	Wind speed	Meter per second (m/s)	DMI	10-minute average, measured 10,00 meters above ground level	Average
			SMHI	10-minute average, once per hour, measured 10,0 m above ground level	
Precipitation	Amount of all precipitation, including rainfall, snowfall etc…	Millimeter (mL)	DMI	total for 1 day	Average
			SMHI	total for 1 hour, once per hour, measured 2,0 m above ground level	

Statistical analysis

To assess the relative importance of local and lagged-up weather conditions recorded along the migration route on the number of Eiders observed at Gedser, a set of competing Generalized Linear Mixed Models (GLMMs) were built using glmmTMB package (version 1.1.13, Brooks *et al.*, 2017)) on R version 4.5.2 (R Core Team, 2025). The Negative Binomial distribution was used over Poisson in order to deal with overdispersion of the residuals (Hervé, 2021).

The impact of local weather was assessed using the temperature, the precipitation, the wind speed and the wind direction measured daily in Gedser only as well as the interaction between the two latest, as fixed explanatory variables. The impact of lagged weather was then tested using the same weather parameters for each lag to build several models, implementing one lag at a time until a full "lagged-only" model was built. Eventually, the combined effect of both local and lagged up-route weather was assessed by adding the weather parameters from all the weather stations to one full model.

<u>Model « Local only » :</u>

Number of Eiders ~ Temperature (0) + Precipitation (0) + Wind speed (0) + Wind direction (0) + Wind speed (0) * Wind direction (0) + (1|Month) + (1|Year)

<u>Models « Lag only » :</u>

Number of Eiders ~ Temperature (x) + Precipitation (x) + Wind speed (x) + Wind direction (x) + Wind speed (x) * Wind direction (x) + [Precipitation (x+1) + Wind speed (x+1) + Wind direction (x+1) + Wind speed (x+1) * Wind direction (x+1) + ……. + Precipitation (5) + Wind speed (5) + Wind direction (5) + Wind speed (5) * Wind direction (5)] + (1|Month) + (1|Year)

<u>Full model (Local + Lags) :</u>

Number of Eiders ~ Temperature (0) + Precipitation (0) + Wind speed (0) + Wind direction (0) + Wind speed (0) * Wind direction (0) + (Precipitation (1) + Wind speed (1) + Wind direction (1) + Wind speed (1) * Wind direction (1) + ……. + Precipitation (5) + Wind speed (5) + Wind direction (5) + Wind speed (5) * Wind direction (5) + (1|Month) + (1|Year)

Multicollinearity was detected visually using pairplots (S4) and statistically using the Variance Inflation Factor (Package R car, version 3.1-3, Fox & Weisberg, 2019) so highly correlated predictors could be removed from the models. The temperature being highly correlated from one station to the other (S4), only one lag-associated temperature was kept per model, with the exception of temperature measured in Gotland (3-days lag). All parameters were normalized to avoid scaling issues and improve numerical stability. To account for any potential unwanted bias due to seasonal differences in the number of migrating individuals per month and over the years, the month and the year were also included as random factors. The performance of all models was then assessed using Akaike Information Criterion (AIC), ΔAIC and Akaike's weight, the model with the lowest AIC considered the best fitted to the data (Package R performance, version 0.14.1, Lüdecke *et al.*, 2021). The coefficients of determination for mixed models marginal R^2 and conditional R^2, representing the proportion of total variance explained with and without random factors respectively, are also displayed.

Eventually, to identify which and how individual weather variables appear to influence migration intensity, the parameter estimates from the previously selected model were used. Whether their effect is significant ($p < 0.05$) was tested using Wald χ^2 test (Fox & Weisberg, 2019).

RESULTS

Migration pattern

As the standardized migration monitoring last 142 days per year (from the 1st of August to the 20th of December) for the past ten years, the initial dataset comprises 1 420 days. Since only the days with a standardized count were kept, the analysis were eventually performed on 1 089 days in total. With an average of 109 ± 41 days per year and a range of [1(2016) ; 132(2019)], the length of the standard period varies considerably.

On average, 128 629 (± 50 597) Eiders are counted each year. On a daily basis, an average of 1 181 (± 2 648) individuals are counted from Gedser Point during autumn migration monitoring, with the migration peak being around half October every year (Figure 2).

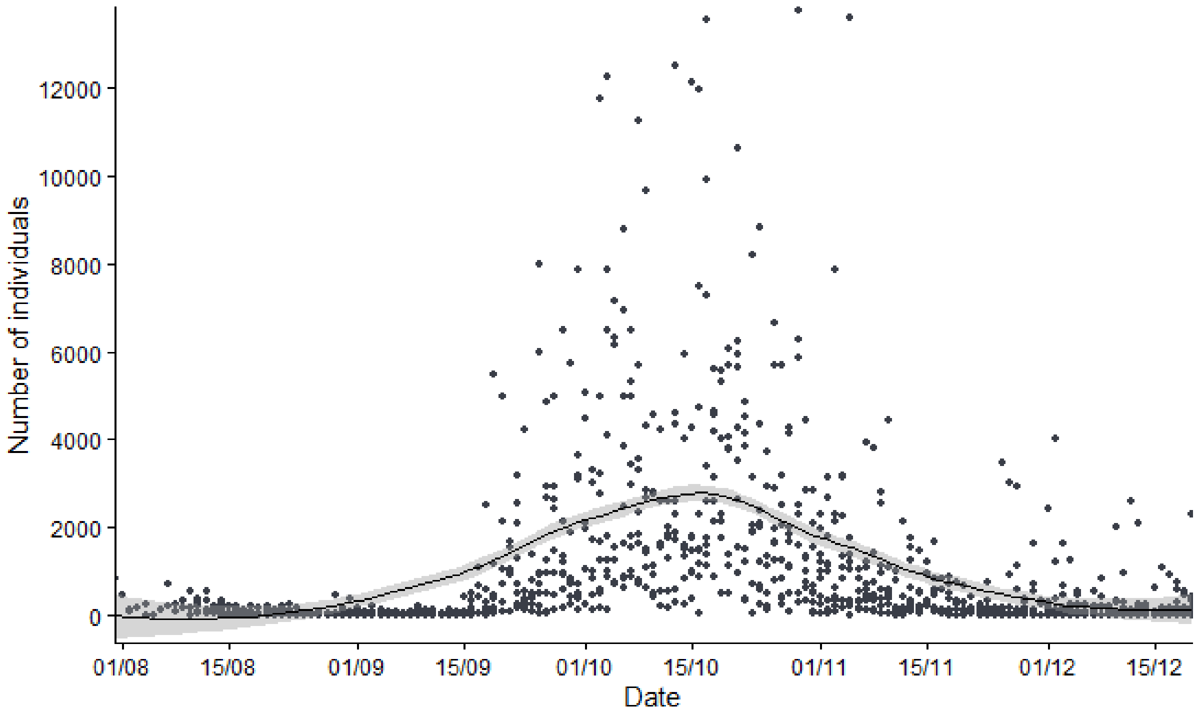


Figure 2 : Daily number of individuals from the 1st of August to the 20th of December since 2016. Yearly average trend is shown in black, with standard error interval in grey.

Weather patterns

In addition to expected seasonal patterns, some lag-associated stations display local ones. The average temperature over the period is 9.88 ± 5.97 °C, with a range of [- 13.6; 24.24]. The temperature decreases over the study period, with the exception of the temperature recorded at Gotland (Figure 3), which remained relatively stable throughout. With an overall daily average of 0.44 ± 2.08 mL, very little precipitation was recorded at most stations exception made with Umeå where the average daily precipitation is 2.31 ± 4.6 mL with a maximum at 44.20 mL (Figure 3). No pattern was detected for wind speed, either over the course of the season or locally (Figure 3). The average wind speed is 5.80 ± 2.72 m/s, and the range is [0.6375; 18.625] m/s. Across the region, the average wind direction is 195.02 ± 79.28°, corresponding to a range between East-Southeasterly and Westerly winds. Wind blows more frequently from the South-West (Figure 3). No local patterns can be identified (Figure 3).

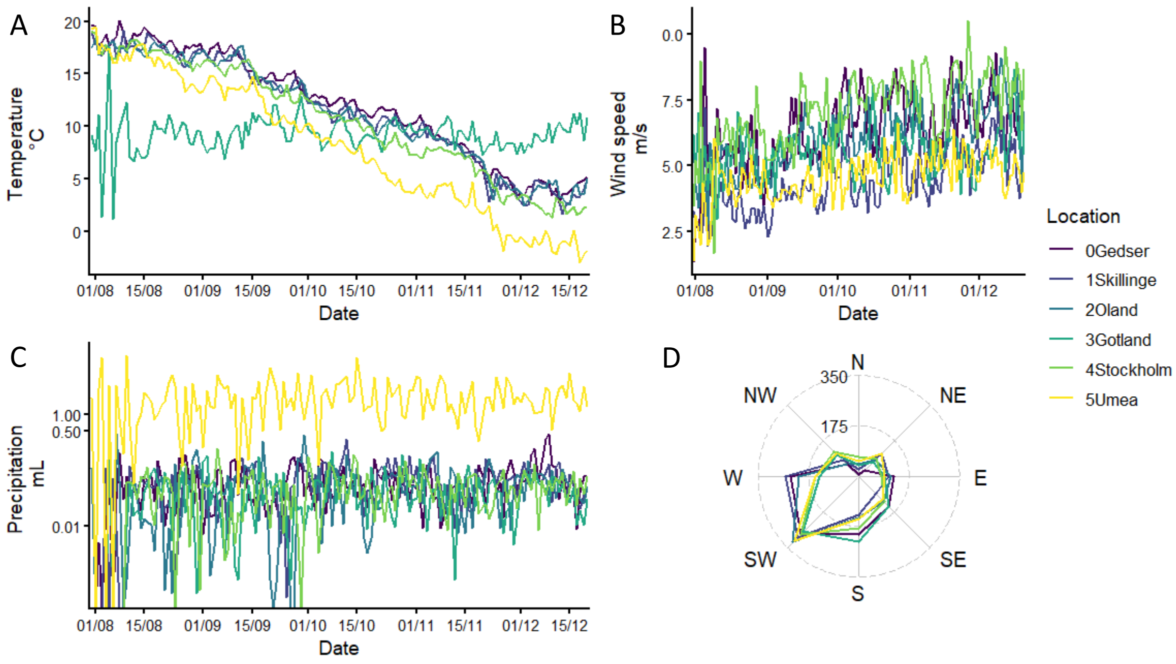


Figure 3 : Patterns of the four weather components at each location from the 1st of August to the 20th of December since 2016. A) Average daily temperature (°C) ; B) Average daily wind speed (m/s) ; C) Average daily precipitation in log scale (mL) ; D) Total number of days for each wind direction. Each colour represents a lag, from the darkest (Local weather at Gedser) to the lightest (5 days lag at Umeå).

Does lagged weather improve the explanation of migration intensity?

A total of 21 models were built (Table 3). Out of all models, the one including only local weather as the highest AIC (15 824.12), while the one including both local and lagged weather (all lags included) has the lowest (14 332.62). All built models explain between 56% and 62% of the variance, with the model including both local and lagged weather having the highest conditional and marginal R2 (Table 3).

Daily weather impact on migration

The impact of weather components on Eiders migratory movements is highly scale dependant. No parameter measured at Umeå, five days before the observation in Gedser, has a significant impact ($p > 0.05$). On every other lag, at least one weather parameter plays a significant role in Eiders migration intensity. The number of individuals increases with the increase of air temperature in Gotland (Figure 4, estimate = 0.65, χ^2 = 6.44, *p* = 0.01) but decrease with the increase of precipitations in Gedser (Figure 4, estimate = -5.57, χ^2= 17.91, *p* = 2.32e-05). Temperature and precipitations have no other significative effect along the migration path (*p* > 0.05). Wind direction has a significant positive impact at both lags 4 and 2 (Figure 4, estimates = 0.15 and 0.82, χ^2 = 4.40 and 5.70, *p* = 0.04 and 0.02 respectively). Wind speed also positively impacts the number of Eiders at lag 1 only (Figure 4, estimate = 1.02, χ^2 = 4.29, *p* = 0.04). The interaction between both wind speed and direction is significative at the local scale only (Figure 4, estimate = -3.41, χ2 = 5.59, *p* = 0.02), and has a negative impact on the number of Eiders migrating. The number of Eiders observed at Gedser therefore decreases as the wind speed and direction increase locally, and the interaction between both makes each other effect stronger.

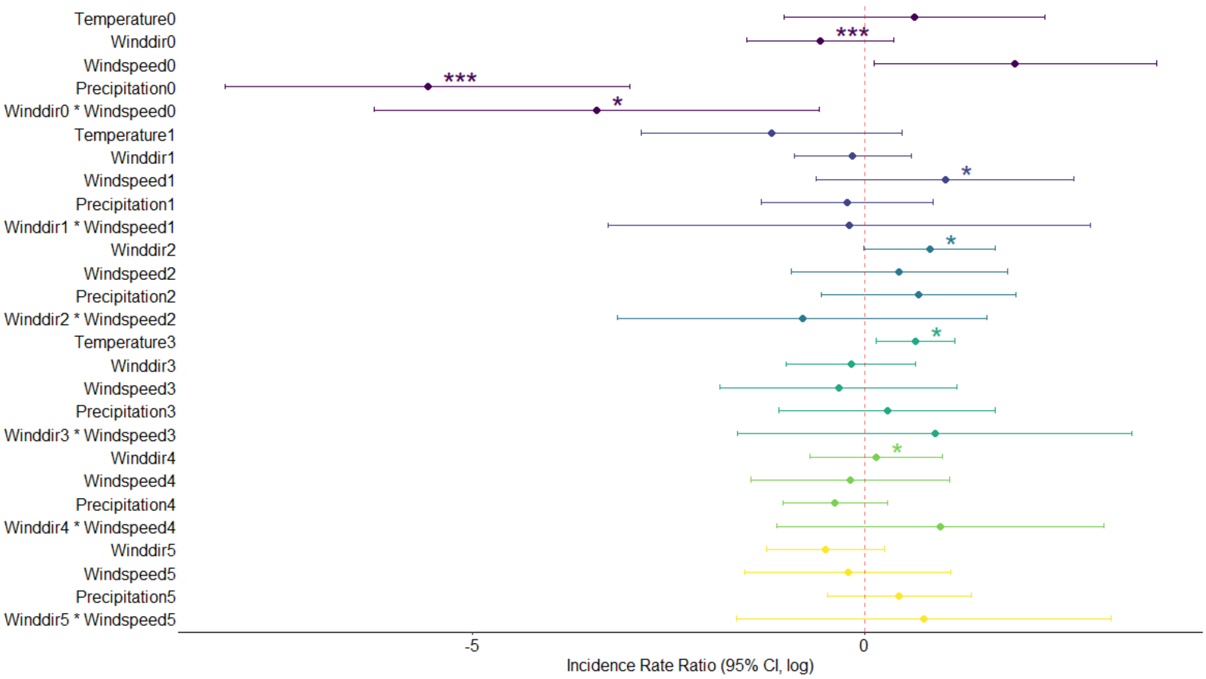


Figure 4 : Effect sizes as Incidence Rate Ratio (exponentiated coefficients), 95% confidence interval and significancy of weather parameters included in the model including both local and lagged weather conditions. Each colour represent a lag, from the darkest (Local weather at Gedser) to the lightest (5 days lag at Umeå). Significancy codes: "***" when *p* < 0.001; "**" when *p* < 0.01; "*" when *p* < 0.05; no symbol when when *p* > 0.05.

Table 3 : Comparison of models performance characterized by Akaike's criterion (AIC), the difference in Akaike's criterion compared with the best model (ΔAIC), Akaike's weight (w), R^2 conditional and R^2 marginal. Lowest AIC and highest R2 conditional are shown in bold. Model's names describe included weather conditions, from local to five-day lags.

Model name	AIC	Δ AIC	AIC weight	R2 conditional	R2 marginal
Local+Lag	**14 332,616**	0,000	1,000E+00	**0,619**	0,102
Local1234	14 359,426	26,810	1,508E-06	0,616	0,095
Lag_only	14 380,971	48,354	3,162E-11	0,585	0,051
Lag1234	14 408,524	75,908	3,287E-17	0,584	0,047
Lag2345	14 503,106	170,489	9,522E-38	0,581	0,042
Lag234	14 533,079	200,463	2,952E-44	0,579	0,034
Local123	14 613,577	280,960	9,779E-62	0,612	0,093
Lag123	14 664,962	332,346	6,793E-73	0,580	0,044
Lag23	14 792,119	459,503	1,660E-100	0,575	0,029
Lag345	14 890,009	557,392	9,200E-122	0,585	0,040
Lag34	14 919,197	586,580	4,224E-128	0,582	0,034
Local12	15 025,234	692,618	3,981E-151	0,613	0,100
Lag12	15 082,104	749,488	1,781E-163	0,571	0,040
Lag3	15 179,255	846,638	1,428E-184	0,580	0,019
Lag45	15 188,916	856,300	1,140E-186	0,583	0,041
Lag4	15 220,693	888,076	1,434E-193	0,578	0,032
Local1	15 433,766	1 101,150	7,734E-240	0,614	0,087
Lag2	15 468,235	1 135,619	2,532E-247	0,567	0,029
Lag1	15 488,274	1 155,658	1,127E-251	0,575	0,029
Lag5	15 820,949	1 488,332	4,941E-324	0,574	0,027
Local_only	15 824,116	1 491,499	0,000E+00	0,588	0,041

DISCUSSION

In this study, the influence of weather was assessed, not only at the local scale of bottleneck observations, but also, and above all, directly from the conditions experienced by the migrating birds along their way. Taking a step back from traditional bottleneck studies, this approach thus allows for assessing and comparing the impacts of weather variables on migration at different spatial and temporal scales.

The relative importance of lagged weather

All built models, regardless of which weather parameters were included, explain Eiders' daily migration intensity better than local weather alone. Migration intensity observed from Gedser therefore appears to reflect processes occurring elsewhere, earlier in the migration journey. Migratory movements are triggered at specific time and place, as answers to conditions experienced by the birds, before they can be observed in Gedser after some delay.

Migrants continuously adjust their behaviour according to intrinsic information, whilst reacting flexibly to environmental conditions along the route (Åkesson & Helm, 2020). From a bottleneck, the number of migrants observed is the result of this continuous decision-making process occurring throughout the migratory journey. The daily numbers can then be interpreted as the concentration of migratory movements at a given time and place. Such a concentration can be explained by the convergence of individual decisions regarding whether to halt or continue migratory movements. These decisions relate to various aspects of the migration journey, such as stopover use, migratory path and overall flight conditions (Åkesson & Hedenström, 2007; Gordo, 2007; Jenni & Schaub, 2003; Shamoun-Baranes *et al.*, 2010). Although intrinsic factors, such as experience (Sergio *et al.*, 2014) or energy reserve (Hedenström, 2008; Klinner *et al.*, 2020) will influence decision-making regarding each of these aspects, environmental conditions play a prominent role in the process. As adverse weather significantly increase energetic costs and risks, migrants adapt their behaviour to avoid such conditions, either by temporarily interrupting their migration (Bauer *et al.*, 2008; Rüppel *et al.*, 2023), by waiting at stopovers for better conditions (Leyrer *et al.*, 2011; Rüppel *et al.*, 2023), or by changing their course or altitude accordingly (Eisaguirre *et al.*, 2018; Senner *et al.*, 2018). Adverse weather also impacts general flight conditions by reducing flight efficiency or by causing drift that migrants must subsequently correct (Åkesson & Hedenström, 2007; Liechti, 2006). Overall migration progress is therefore significantly slowed down in the event of unfavourable conditions. Conversely, the occurrence of favourable conditions increases the departure probability from a stopover (Dänhardt & Lindström, 2001; O'Neal *et al.*, 2018; Vanausdall *et al.*, 2024). Such suitable conditions can also greatly increase flight efficiency (Åkesson & Hedenström, 2007), allowing migrants to save both time and energy. Consequently, mass departures and concentrated migratory movements would be observed when weather conditions are suitable, or suitable enough after prolonged period of bad weather (Benjumea *et al.*, 2024; Erni *et al.*, 2002; Leyrer *et al.*, 2011; Shamoun-Baranes *et al.*, 2017). This phenomenon, known as "tap effect" or tailbacks ("*Zugstau*") is the visible consequence of converged individual decision making process in answer to similar environmental conditions experienced along the route.

At Gedser, the daily number of migrating Eiders is the result of their decisions continuously taken along the way. As local weather conditions, from the observer perspective, have not yet been encountered by the migrating individuals, they do not fully reflect their experience, nor the factors directly influencing their behaviour and decision-making. Meanwhile, lagged weather is an essential part of *en route* conditions, and therefore represent important clues in that matter. Lagged weather influence migration aspects at multiple scales, not only *en route* (Åkesson & Helm, 2020; Underhill & Remisiewicz, 2025), but also at stopover sites (Haest *et al.*, 2019; Weber *et al.*, 1999), or even directly at the breeding grounds (Haest *et al.*, 2019; Shamoun-Baranes *et al.*, 2006). When compared to traditional approaches using local meteorological data as main explanatory variables, time-window analysis using lagged weather has also proved more effective at predicting behaviours other than migration, such as roosting phenology (Deng *et al.*, 2025). Although Morales-Góngora *et al.* (2025) found no effect of lagged weather, they point out that such effect would better be assessed using weather variables measured not at the same geographical scale that the observations, but elsewhere on the migration route. The importance of lagged weather on migrants daily counts have been highlighted in similar studies conducted at other bottleneck sites, with a focus on soaring birds and long distance migrants (Benjumea *et al.*, 2024; Miller *et al.*, 2016). This result is, however, not consistent from one site to another, as lagged weather conditions do not always outperform local ones in the prediction of daily counts (Miller *et al.*, 2016). Moreover, as the atmosphere is a connected air mass, atmospheric dynamics could provide migrants with information on what to expect further along their trajectory (Shamoun-Baranes *et al.*, 2010). They could consequently adapt their behaviour to both experienced and expected weather conditions, increasing the explanatory power of local weather conditions from the bottleneck perspective.

The conditions experienced *en route* are therefore good indicators of the migratory movements observed from a bottleneck, and it is essential to take them into account in such analysis. The study of the impact of the weather on migratory movements must be approached from a multi-scale perspective, considering not only local conditions but also, and above all, parameters upstream of the observation sites.

The role of weather in Eiders migration

It is thus in the occurrence of relatively favourable conditions that significant migratory movements can be expected, with all individuals migrating within the same time-windows. The number of individuals observed from a fixed spot will in turn increase due to high concentration of movements. In this study, the meteorological parameters that appear to favour such events, and thus the number of individuals seen at Gedser, are wind speed, wind direction and temperature experienced at different places along the way.

No effect of weather on daily numbers was found at five-day lag scale (Umeå). At both four-day lag (Stockholm) and two-day lag (Öland), a positive effect of wind direction was highlighted. Temperature also has a positive effect on the number of Eiders observed in Gedser at three-day lag scale (Gotland), as does wind speed at one-day lag scale (Skillinge). As for local weather conditions (Gedser), such as precipitation and the interaction between wind speed and wind direction, they have an adverse effect on the number of individuals observed.

Wind

Wind speed measured in Skillinge (1 day lag), regardless of associated wind direction, positively impacts Eiders' migration intensity. It means that the stronger the wind is when the

Eiders fly by the area, regardless of the wind direction, the higher their numbers are the next day in Gedser. In contrast with our expectations, neither the wind direction nor the interaction between wind speed and wind direction are significant at this location. Wind speed was expected to not have the same impact on Eiders' migration depending on the wind direction, as the individuals would supposedly react differently to a strong supportive tailwind than to a strong headwind or a drift-causing sidewind. Strong headwinds are usually found unfavourable for flight or departure from stopovers (O'Neal *et al.*, 2018; Rüppel *et al.*, 2023), while weak winds are clues for suitable take-off and flight conditions (Liechti, 2006; Schaub *et al.*, 2004). A positive relationship between wind strength and migration intensity is therefore an unexpected result in two respects.

However, when investigated independently, a correlation between wind speed and wind direction has been found at Skillinge scale (S2). Indeed, Eastern-coming wind are significantly stronger than other directions, and winds from Northwest are significantly weaker than the others. No differences can be found for every other direction. This nonlinear relation seems to have no impact on multicollinearity in the tested model, which would explain why no effect of wind direction or the interaction have been found in this analysis. With such relation, the observed effect would therefore not be an effect of wind speed, but indirectly of wind direction.

Wind direction is often described as the main factor influencing migrants decision-making process (Alerstam, 1979; Liechti, 2006) and is therefore more investigated than wind speed. By selecting supportive winds, migrants can indeed save large amount of time and energy (Becciu *et al.*, 2023; Bruderer & Liechti, 1998; Weber *et al.*, 1998), which is essential to successfully survive through migration. Therefore, tailwinds tend to favour migratory movements and stopover departures while headwinds negatively impact both departure probability and migration speed (Erni *et al.*, 2002; Haest *et al.*, 2019; Rüppel *et al.*, 2023). When flying by Skillinge in direction to Gedser, Eiders are flying toward the West or the South-West (Figure 1.A). In this context, strong Easternly winds are tailwinds. The positive relationship between strong Easternly winds and the migration intensity could therefore be explained by their supportive aspect.

The number of Eiders seen in Gedser is correlated with wind direction measured two and four days before the observation date. A positive effect of wind direction means that the migration of Eiders is favoured when they encounter Westerly or North-westerly winds whilst passing off the coast of Stockholm (4 days lag) and near Öland (2 days lag). At these locations, Westerly and North-Westerly winds blow perpendicular to the route taken during post-breeding migration (Figure 1.A). The migration intensity observed at Gedser therefore seems not to be favoured by tailwinds at these scales, as expected, but by winds that could potentially cause drift away from their intended course. This finding is surprising, as most studies have highlighted the tendency of migrants to avoid crosswinds (Åkesson & Hedenström, 2007; Liechti, 2006), which can blow them off course and thus require them to expend additional energy by compensating (Aurbach *et al.*, 2020; Werfeli *et al.*, 2022). Albeit some species display great tolerance to crossflows (Åkesson & Hedenström, 2007; Liu & Swanson, 2015; Tsvey *et al.*, 2007) which would therefore not have significant impact on their migration, Eiders' migratory intensity seems to beneficiate from drift-causing winds. However, in this context, Easterly or Southeasterly winds would also cause the birds to drift, this time ever closer to land. Eiders migrate along the coast but rarely venture over land, preferring to fly over bodies of water (Masden *et al.*, 2009). We can therefore expect that winds from directions pushing them towards land, such as those from the East and South-East, would have a more negative impact on flight conditions and on the effort required to reroute than Westerly or North-Westerly winds, which cause drift out to sea.

This effect is yet not observed at lags other than 2 days lag and 4 days lag, which means that wind direction has no impact on migration intensity in between both, at 3 days lag. Such results contrast with other studies conducted at bottleneck scale, which have highlighted the influence of weather conditions on migration especially three days before the observation date (Benjumea *et al.*, 2024; Miller *et al.*, 2016). The lack of effect at this specific scale could be explained by the geographical position of the island of Gotland, located 86 km off the East coast of Sweden. Given that Eiders do not appear to be affected by either headwinds or tailwinds, drift-causing winds in this area would not significantly divert the birds from their course. In fact, those winds would in any case allow the migrants to either follow a coastline or fly out to sea, both options being regularly observed for that species.

Temperature

Some of the weather conditions experienced by migratory birds near Gotland still play a part in the intensity of migration observed at Gedser. Temperature, in particular, appears to have a significant positive effect, meaning that a rise in temperature leads to an increase in the number of birds counted three days later at Gedser. Temperature fluctuations on Gotland therefore cause mass accumulations or departures of birds. Temperature plays a significant role in the onset of migration, decreasing temperatures being often used by migrants as a signal to leave the breeding grounds (Haest *et al.*, 2019; Jenni & Kéry, 2003). Temperature is therefore more often depicted as a global factor influencing species phenology (timing of migration) rather than an *en route* cue causing daily variation in the number of individuals. However, experienced temperature still influences migrants' ability to fly. Indeed, long-distance migratory flights are highly energy-consuming, thereby causing important increase in body temperature (Guillemette *et al.*, 2016, 2017). In addition to refuelling and avoiding adverse weather conditions, stopovers also provide migrants the necessary time to cool down, hence avoiding hyperthermia (Guillemette *et al.* 2016 ; 2017). Increase in air temperature can therefore have a negative impact on migrants' numbers, forcing them to increase the number of necessary pauses along the migration path. Similarly, individuals decisions to migrate or to take off from stopover sites are either associated with decrease in air temperature (Benjumea *et al.*, 2024; Berthold, 2001), or poorly influenced by temperature (Benjumea *et al.*, 2024; Vanausdall *et al.*, 2024), depending on the species and the studied period. Schmaljohann *et al.* (2017) have found a timing specific relationship between temperature and Wheatear (*Oenanthe oenanthe*) departure from a stopover, the latest being negatively influenced by air temperature at the beginning of the migrating season, but positively influenced by it toward the end.

The positive relationship between temperature in Gotland and migration intensity therefore mainly contrast with previous findings on the matter. Such result raises questions, particularly regarding the potential use of the area by Eiders. Whether they use the area as a stopover or only fly over it remains uncertain, making it difficult to draw clear conclusions about the reasons behind this positive association between temperature and migration intensity. Moreover, temperature appears to influence migratory movements exclusively at the 3 days lag scale. Temperature was not included as an explanatory variable in the models for each of the measured lags due to high autocorrelation from one day to the next. Indeed, the study period runs from August to December, with significant but consistent seasonal variations among the different locations. Across the entire study area, temperatures are therefore higher in August and decline steadily until the end of December. This pattern is observed at every weather station included in the study, with the exception of Gotland where temperatures remain strangely constant throughout the study period. This result should therefore be treated with caution, and it would be worthwhile to explore in greater depth the reasons that might explain the absence of seasonal variation in temperature at this specific scale.

Umeå (lag 5) weather

Weather parameters therefore impact migration intensity at every step of the flyway, with however the exception of 5 days lag. Surprisingly, weather seems to have no influence at the furthest point from the bottleneck. Such influence has yet been found at very large time scales, sometimes at both intra and inter annual scales (Clements *et al.*, 2022; Haest *et al.*, 2018, 2019). The lack of impact of weather parameters at this location can be interpreted in different ways. As migrants decisions-making process is continuous and weather conditions can variate a lot along the way, behavioural adaptations made earlier in the migration progress could get overshadowed by following decisions. Thus, migration intensity as observed from the bottleneck perspective would be the result of the most recent decisions only and would not allow to trace back to earlier decisions. However, this hypothesis is to be tempered by previously discussed results, as the analysis allows to highlight weather impact up to four days before the observation date.

Alternatively, the lack of impact at this location could reflect differences between the presumed migratory path and the actual route taken by migrating Eiders. In order to simplify both the dataset and the analyses, focus has been made on Eiders migrating towards Gedser along the Swedish coasts from their breeding grounds in the Gulf of Bothnia. Lagged data has been collected under this hypothesis. However, a part of the population migrating by Gedser breed in the Gulf of Finland rather than upper North, and might be taking another itinerary before being observed at Gedser. Therefore, weather data sampled in Stockholm or in Umeå, do not impact migratory movements of an unknown proportion of the studied population. No conclusion can therefore be drawn about whether large scale weather impacts migratory movements, as relevant parameters might need to be measured elsewhere along the migration path. Future work focusing on more precise assessment of those paths and flyways used by the Baltic/Wadden sea Eiders population would allow to put this result in perspective and improve our understanding of the impact of weather on Eiders' migration at even larger temporal and spatial scales.

Local weather

If implementing lagged meteorological data is essential to correctly assess the correlation between weather conditions and migration intensity, relying solely on such data is not sufficient to obtain the best possible overview. Compared to other combinations of parameters, lagged weather only is not performing nearly as good as combined lagged and local weather when it comes to explain migration intensity. From the best identified model, it has been shown that local weather also impacts daily migration intensity at Gedser, but in a different way compared to lagged weather.

While wind from Westerly direction the previous days (lag 2 and lag 4) positively impact the number of Eiders counted, and a positive relationship was also found with the wind speed experienced by the birds the day before being seen in Gedser, similar wind conditions at the local scale has the opposite effect. At Gedser, the interaction between wind speed and wind direction has a negative impact on migration intensity. This result implies that, at a given direction, stronger winds are correlated with fewer individuals, and so are Westerly and North-westerly winds compared to other directions at a given speed. When flying by Gedser Point during post breeding migration, Eiders are mainly heading West towards their wintering grounds. Westerly and North-Westerly winds can therefore be considered headwinds at this location. As already mentioned, such winds can make it harder for migrants to fly, especially when the wind speed increase. When propensity of those adverse conditions increases, it is therefore not surprising to see less birds. Indeed, it would be expected that the migrants would either rest and wait for better flying conditions, or struggle to fly, both options causing the number of birds observed in Gedser to be less important than during optimal conditions.

Similarly, precipitation also has a negative impact on Eider's daily migration intensity, meaning that less individuals would be seen in increasing rainfalls. The adverse effect of precipitation is commonly observed among migrating birds, with increased migration intensity or migration rate in low or no rain (Benjumea *et al.*, 2024; Erni *et al.*, 2002). Similarly, departures from stopovers are more likely to happen in absence of precipitation (Aurbach *et al.*, 2020; Rüppel *et al.*, 2023), although it is not always the case (Shamoun-Baranes *et al.*, 2017). In addition to reducing visibility and orientation performance, rainfall can significantly weigh the birds down and consequently increase their energy expenditure (Richardson, 1978). Waiting for better conditions being therefore more advantageous than to pursue migration, it is not surprising to observe less migrants on rainy days.

However, local weather conditions actually have a dual role : they impact both the migration conditions, as experienced by the birds, and the observation conditions, as perceived by migration monitors. The standard protocol for migration monitoring at Gedser Point states that migration counts should not be carried out when observation conditions deteriorate due to rain, fog, snowfall, storms or similar conditions (Kayser, 2024). Consequently, days with favourable weather conditions are present in higher numbers in the dataset, and days with adverse weather conditions have higher propensity to be considered as "zero days". This bias might be increasing already existing trends in the correlation between adverse weather conditions and low records of Eiders, with both wind and rain conditions.

Strengths and limitations

Data collection

While conducting a count at a bottleneck site is extremely beneficial, as it concentrates the flows of species and individuals in a single location over known time periods, thereby enabling the collection of a large amount of data, standard protocols must be established while keeping in mind what is practically reasonable. Choices are made regarding the time period covered, both yearly and daily, in order to ensure healthy work conditions for the birdwatchers, a representative picture of the migration process, as well as consistency and reproducibility from one year to the next. Eiders migratory behaviours can be observed as early as late June, with mostly males and non-breeding individuals (Alerstam & Högstedt, 1982; Salomonsen, 1968). As this period is excluded from the standard protocol for monitoring post-nuptial migration, the weather conditions that favour these early migratory movements, although very different from those typically encountered in autumn, were therefore not considered in this analysis. Even during the standard period, daily effort is put onto morning counts when migratory movements are supposedly more intense. Those five hours count are actually only a snapshot of the theoretical migration hours available for the Eider per day. Migration happens throughout the entire day, with sometimes peaks in intensity in both morning and afternoon. This limitation is overcome by considering daily counts and weather variables at a daily resolution, but the potential for assessing more detailed interaction between weather and migratory movements is then diminished.

The choice of weather variables was based on a priori assumptions regarding the parameters likely to influence Eider migration. Other parameters with greater biological significance regarding the studied species could have been included, or weather variables could have been selected without using any a priori assumptions to avoid bias or unwanted noise in the statistical models (Van De Pol *et al.*, 2016). However those choices were motivated both by the time required to collect meteorological data, which would have largely increase in case of following Van de Pol's methodology, and by the desire for replicability. Indeed, the selected variables (Temperature, Precipitation and Wind-related variables) are widely used in studies investigating the impact of weather on both pre-nuptial and post-nuptial migration (Haest *et al.*, 2019), therefore allowing comparison on their effect on different studied species and time period.

The choice of weather stations and the collection of lagged data has been conducted based on assumptions about the daily distance covered by Eiders. Although the daily distance travelled have been estimated using conclusions from several studies, there is no certainty about the exact position of Eiders during their migration, and consequently about the weather they really experience. Moreover, weather conditions can also variate between coastal and offshore locations, or between high altitudes and close to the waves (Klinges *et al.*, 2026). All those variations at reduce scale make it harder to evaluate precisely the conditions experienced by migrants when studied from a bottleneck observation site. Future studies on this population could benefit from movement data collection, using telemetry for example, to gain a clear understanding of the weather conditions the birds are facing and thereby improve future analyses.

Model limitations

Despite the ecological interest of implementing many weather parameters as an attempt to get the best overview of potential influences of Eiders migration, conducting such complete studies can have negative impact on the statistical power of the analysis. In order to conduct strong analysis and ensure statistical power, further studies could either improve the size of the dataset or reduce the number of weather variables tested. The dataset size can be improved with the collection of more data by maintaining the sampling effort at Gedser. Regarding the number of weather variables, a weather index summarizing information from different weather components could be used as it has been done with the Normalized Difference Vegetation Index (NDVI), or the North Atlantic Oscillation (NAO) in Clements *et al.* (2022) or with the Weather Severity Index (WSI) in Aagaard *et al.* (2022). Although this method would make it possible to overcome certain constraints regarding the size of the dataset, the direct causality of certain weather components could not be properly assessed. The choice must therefore be based on the objective of the study and on the balance between the quality of the analysis and the desired level of detail.

In addition to sample size limitations, the use of Generalized Linear Mixed Models to conduct such analysis can also be discussed. Indeed, relationships between environmental conditions and living being's responses are not always linear (Robertson *et al.*, 2024). Numerous studies on the effect of temperature on organisms highlight that individual responses to rising temperatures can take many forms (Arroyo *et al.*, 2022; Kingsolver *et al.*, 2015). They demonstrate the existence of thermal optima and non-linear performance. Similarly, migrants flight performance can be positively influenced by wind speed up to some extent. Strong winds can indeed promote migration efficiency, but stormy conditions might have adverse effects (Alerstam, 1979; Leyrer *et al.*, 2011). It might therefore be worthwhile to conduct this study on the assumption that the migratory activity of Eiders do not increase or decrease linearly along weather conditions variations, but with an optimum that is still yet to be identified.

CONCLUSION

Birds’ migratory decision-making process is heavily influenced by the weather conditions encountered *en route*, primarily by wind-related parameters. As all weather parameters vary simultaneously, both temporally and spatially, migratory behaviour can only be understood by considering their combined and continuous effects on migrants. Thus, lagged weather is essential to fully understand associated behaviours, even from a bottleneck perspective. This study complements previous ones in demonstrating the value of bottlenecks as relevant tools for studying migration from a distance, providing information not only on migrants population dynamics but also on species ecology. Eiders remain a largely understudied species, particularly with regard to their migratory ecology. Improving our knowledge on this matter not only enhances our understanding of this species but may also serve as a basis for future studies on other species using the Baltic/Wadden migratory flyway. This study also provides a great framework for future interpretation of migrants numbers and movements both at Gedser and at other water-associated birds migration monitoring places. Like many migratory species, waterbirds can be significantly affected by climate change. Potential impacts of climate change still remain uncertain, but these effects may manifest themselves through the occurrence of exceptional weather conditions altering the decisions and behaviour of migrants *en route*, or, for example, through changes in the food resources available along the route. In this regard, it is important to maintain sampling efforts along migration routes and to keep improving our knowledge about how migrants use their habitats on their way.

REFERENCES

Aagaard, K. J., Lonsdorf, E. V., & Thogmartin, W. E. (2022). Effects of weather variation on waterfowl migration : Lessons from a continental-scale generalizable avian movement and energetics model. *Ecology and Evolution*, *12*(2), e8617. https://doi.org/10.1002/ece3.8617

Åkesson, S., & Hedenström, A. (2007). How Migrants Get There : Migratory Performance and Orientation. *BioScience*, *57*(2), 123-133. https://doi.org/10.1641/B570207

Åkesson, S., & Helm, B. (2020). Endogenous Programs and Flexibility in Bird Migration. *Frontiers in Ecology and Evolution*, *8*. https://doi.org/10.3389/fevo.2020.00078

Alerstam, T. (1979). Wind as Selective Agent in Bird Migration. *Ornis Scandinavica (Scandinavian Journal of Ornithology)*, *10*(1), 76-93. https://doi.org/10.2307/3676347

Alerstam, T. (1993). *Bird Migration*. Cambridge University Press.

Alerstam, T. (2011). Optimal bird migration revisited. *Journal of Ornithology*, *152*(S1), 5-23. https://doi.org/10.1007/s10336-011-0694-1

Alerstam, T., & Högstedt, G. (1982). Bird Migration and Reproduction in Relation to Habitats for Survival and Breeding. *Ornis Scandinavica (Scandinavian Journal of Ornithology)*, *13*(1), 25-37. https://doi.org/10.2307/3675970

Alerstam, T., & Lindström, Å. (1990). Optimal Bird Migration : The Relative Importance of Time, Energy, and Safety. In E. Gwinner (Éd.), *Bird Migration* (p. 331-351). Springer. https://doi.org/10.1007/978-3-642-74542-3_22

Amaral, B. R., Youngflesh, C., Tingley, M., & Miller, D. A. W. (2025). Shifting Gears in a Shifting Climate : Birds Adjust Migration Speed in Response to Spring Vegetation Green-Up. *Diversity and Distributions*, *31*(5), e70033. https://doi.org/10.1111/ddi.70033

Amélineau, F., Delbart, N., Schwemmer, P., Marja, R., Fort, J., Garthe, S., Elts, J., Delaporte, P., Rousseau, P., Duraffour, F., & Bocher, P. (2021). Timing of spring departure of long distance migrants correlates with previous year's conditions at their breeding site. *Biology Letters*, *17*(9), 20210331. https://doi.org/10.1098/rsbl.2021.0331

Arroyo, J. I., Díez, B., Kempes, C. P., West, G. B., & Marquet, P. A. (2022). A general theory for temperature dependence in biology. *Proceedings of the National Academy of Sciences*, *119*(30), e2119872119. https://doi.org/10.1073/pnas.2119872119

Aurbach, A., Schmid, B., Liechti, F., Chokani, N., & Abhari, R. (2020). Simulation of broad front bird migration across Western Europe. *Ecological Modelling*, *415*, 108879. https://doi.org/10.1016/j.ecolmodel.2019.108879

Bauer, S., Van Dinther, M., Høgda, K.-A., Klaassen, M., & Madsen, J. (2008). The consequences of climate-driven stop-over sites changes on migration schedules and fitness of Arctic Geese. *Journal of Animal Ecology*, *77*(4), 654-660.

Becciu, P., Troupin, D., Dinevich, L., Leshem, Y., & Sapir, N. (2023). Soaring migrants flexibly respond to sea-breeze in a migratory bottleneck : Using first derivatives to identify behavioural adjustments over time. *Movement Ecology*, *11*(1), 44. https://doi.org/10.1186/s40462-023-00402-4

Benjumea, R., Astrain, C., Istúriz, A., Oria, P. A., Ibarrola, I., & del Mar Delgado, M. (2024). Weather conditions at different spatial and temporal scales influence avian post-breeding migration patterns on route. *Journal of Zoology*, *323*, 305-316. https://doi.org/10.1111/JZO.13178

Berthold, P. (2001). *Bird Migration : A General Survey*. Oxford University Press. https://doi.org/10.1093/oso/9780198507864.001.0001

BirdLife International. (2018). *Common Eider Somateria Mollissima Species Factsheet*. BirdLife DataZone. https://datazone.birdlife.org/species/factsheet/common-eider-somateria-mollissima

Borkenhagen, K. (2020). *Seabird Monitoring in the German North Sea and Baltic Sea 2020*.

Brooks, M. E., Kristensen, K., Benthem, K. J. van, Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Mächler, M., & Bolker, B. M. (2017). glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal*, *9*(2), 378-400. https://doi.org/10.32614/RJ-2017-066

Bruderer, B., & Liechti, F. (1998). Flight Behaviour of Nocturnally Migrating Birds in Coastal Areas : Crossing or Coasting. *Journal of Avian Biology*, *29*(4), 499-507. https://doi.org/10.2307/3677169

Buechley, E. R., Beatty, W., Nikolov, S., Dobrev, V., Arkumarev, V., Saravia, V., Bougain, C., Bounas, A., Kret, E., Skartsi, T., Aktay-Sözüer, L., Aghababyan, K., Frehner, E., & Sekercioglu, C. (2018). Identifying critical migratory bottlenecks and high-use areas for an endangered migratory soaring bird across three continents. *Journal of Avian Biology*, *49*, e01629. https://doi.org/10.1111/jav.01629

Buechley, E. R., Oppel, S., Efrat, R., Phipps, W. L., Carbonell Alanís, I., Álvarez, E., Andreotti, A., Arkumarev, V., Berger-Tal, O., Bermejo Bermejo, A., Bounas, A., Ceccolini, G., Cenerini, A., Dobrev, V., Duriez, O., García, J., García-Ripollés, C., Galán, M., Gil, A., … Marra, P. P. (2021). Differential survival throughout the full annual cycle of a migratory bird presents a life-history trade-off. *Journal of Animal Ecology*, *90*(5), 1228-1238. https://doi.org/10.1111/1365-2656.13449

Cardenas-Ortiz, L., Bayly, N. J., Kardynal, K. J., & Hobson, K. A. (2020). Defining catchment origins of a geographical bottleneck : Implications of population mixing and phenological overlap for the conservation of Neotropical migratory birds. *The Condor: Ornithological Applications*, *122*(2), duaa004. https://doi.org/10.1093/condor/duaa004

Cerro, R. de la T., Misra, G., Gleeson, E., Serbin, G., Zimmermann, J., Cawkwell, F., Wingler, A., & Holloway, P. (2025). Modelling asynchrony in phenology considering a dynamic representation of meteorological variables. *PeerJ*, *13*, e18653. https://doi.org/10.7717/peerj.18653

Christensen, T. K. (2008). *Factors affecting population size of Baltic Common Eiders* Somateria mollissima [PhD Thesis]. University of Aarhus, Denmark.

Clements, S. J., Loghry, J. P., Ballard, B. M., & Weegman, M. D. (2022). Carry-over effects of weather and decision-making on nest success of a migratory shorebird. *Ecology and Evolution*, *12*(12), e9581. https://doi.org/10.1002/ece3.9581

Dänhardt, J., & Lindström, Å. (2001). Optimal departure decisions of songbirds from an experimental stopover site and the significance of weather. *Animal Behaviour*, *62*(2), 235-243. https://doi.org/10.1006/anbe.2001.1749

Danish Meteorological Institute (2026) DMI Open Data QGIS plugin. Version 1.0.9. URL: https://github.com/dmidk/Open-Data-QGIS-plugin

Day, R., Rose, J., Cooper, B., & Blaha, R. (2000). *Migration Rates and Flight Behavior of Migrating Eiders Near Towers at Barrow, Alaska*.

Day, R., Rose, J., Prichard, A., Blaha, R., & Cooper, B. (2004). Environmental Effects on the Fall Migration of Eiders *Somateria Spp* at Barrow, Alaska. *Marine Ornithology*, *32*(1). https://doi.org/10.5038/2074-1235.32.1.593

Delfino, H. C. (2024). Stormy Skies and Feathered Lives : Synthesizing the Effects of Adverse Meteorological Events on Avian Physiology, Behavior, and Ecology. *Ornithological science*, *23*(2), 103-117. https://doi.org/10.2326/OSJ.23.103

Deng, Y., Haest, B., Belotti, M. C. T. D., Zhao, W., Pérez, G., Tielens, E., Sheldon, D., Maji, S., & Kelly, J. F. (2025). Continental Connections : Changing Temperature, Wind and Precipitation Advance the Postbreeding Roosting Phenology of Avian Aerial Insectivores. *Global Ecology and Biogeography*, *34*, e70052. https://doi.org/10.1111/GEB.70052

Desholm, M., Christensen, T. K., Scheiffarth, G., Hario, M., Andersson, Å., Ens, B., Camphuysen, C. J., Nilsson, L., Waltho, C. M., Lorentsen, S.-H., Kuresoo, A., Kats, R. K. H., Fleet, D. M., & Fox, A. D. (2002). Status of the Baltic/Wadden Sea population of the Common Eider *Somateria m. Mollissima* . *Wildfowl*, *53*, 167-203.

Dillenseger, G., Sparkes, C. H. J., Székely, T., Sandercock, B. K., Freckleton, R. P., & Kubelka, V. (2026). Global analysis of annual survival among shorebirds reveals a negative effect of migration distance and a decline in recent decades. *Oikos*, e11931. https://doi.org/10.1002/oik.11931

DOF. (2026). *DOFbasen—Af Dansk Ornitologisk Forening*. Data. https://dofbasen.dk/search/result.php?design=table&soeg=soeg&obstype=observationer&species=alle&subspecies=yes&sortering=art&artdata=art&hiddenart=02060&omraade=l

okalitet&hiddenlok=395007&periode=mellemdato&dato_first=01-01-1800&dato_second=31-12-2026&obserdata=4874GFU

Eisaguirre, J. M., Booms, T. L., Barger, C. P., McIntyre, C. L., Lewis, S. B., & Breed, G. A. (2018). Local meteorological conditions reroute a migration. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1890), 20181779. https://doi.org/10.1098/rspb.2018.1779

Ekroos, J., Fox, A. D., Christensen, T. K., Petersen, I. K., Kilpi, M., Jonsson, J. E., Green, M., Laursen, K., Cervencl, A., Boer, P. de, Nilsson, L., Meissner, W., Garthe, S., & Öst, M. (2012). Declines amongst breeding Eider *Somateria mollissima* numbers in the Baltic/Wadden Sea flyway. *Ornis Fennica*, *89*(2), 81-90. https://doi.org/10.51812/of.133795

Erni, B., Liechti, F., Underhill, L., & Bruderer, B. (2002). Wind and rain govern the intensity of nocturnal bird migration in central Europe—A log-linear regression analysis. *Ardea*, *90*, 155-166.

Filippi-Codaccioni, O., Moussus, J.-P., Urcun, J.-P., & Jiguet, F. (2010). Advanced departure dates in long-distance migratory raptors. *Journal of Ornithology*, *151*(3), 687-694. https://doi.org/10.1007/s10336-010-0500-5

Flack, A., Aikens, E. O., Kölzsch, A., Nourani, E., Snell, K. R. S., Fiedler, W., Linek, N., Bauer, H.-G., Thorup, K., Partecke, J., Wikelski, M., & Williams, H. J. (2022). New frontiers in bird migration research. *Current Biology*, *32*(20), R1187-R1199. https://doi.org/10.1016/j.cub.2022.08.028

Fox, J., & Weisberg, S. (2019). *An R Companion to Applied Regression*. Third edition. Sage,. https://www.john-fox.ca/Companion/

Gordo, O. (2007). Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. *Climate Research*, *35*, 37-58. https://doi.org/10.3354/cr00713

Guillemette, M., Polymeropoulos, E., Portugal, S., & Pelletier, D. (2017). It Takes Time to Be Cool : On the Relationship between Hyperthermia and Body Cooling in a Migrating Seaduck. *Frontiers in Physiology*, *8*, 532. https://doi.org/10.3389/fphys.2017.00532

Guillemette, M., Woakes, A. J., Larochelle, J., Polymeropoulos, E., Granbois, J.-M., Butler, P. J., Pelletier, D., Frappell, P. B., & Portugal, S. J. (2016). Does hyperthermia constrain flight duration in a short-distance migrant? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1704), 20150386. https://doi.org/10.1098/rstb.2015.0386

Haest, B., Hüppop, O., & Bairlein, F. (2018). The influence of weather on avian spring migration phenology : What, where and when? *Global Change Biology*, *24*(12), 5769-5788. https://doi.org/10.1111/gcb.14450

Haest, B., Hüppop, O., Van De Pol, M., & Bairlein, F. (2019). Autumn bird migration phenology : A potpourri of wind, precipitation and temperature effects. *Global Change Biology*, *25*(12), 4064-4080. https://doi.org/10.1111/gcb.14746

Hanssen, S. A., Gabrielsen, G. W., Bustnes, J. O., Bråthen, V. S., Skottene, E., Fenstad, A. A., Strøm, H., Bakken, V., Phillips, R. A., & Moe, B. (2016). Migration strategies of common Eiders from Svalbard : Implications for bilateral conservation management. *Polar Biology*, *39*(11), 2179-2188. https://doi.org/10.1007/s00300-016-1908-z

Harrison, X. A., Blount, J. D., Inger, R., Norris, D. R., & Bearhop, S. (2011). Carry-over effects as drivers of fitness differences in animals : Carry-over effects in animal populations. *Journal of Animal Ecology*, *80*(1), 4-18. https://doi.org/10.1111/j.1365-2656.2010.01740.x

Hedenström, A. (2008). Adaptations to migration in birds : Behavioural strategies, morphology and scaling effects. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *363*(1490), 287-299. https://doi.org/10.1098/rstb.2007.2140

HELCOM Red List. (2024). *Species information Sheet*—Somateria mollissima.

Hervé, M. (2021). *Aide-mémoire de statistique appliquée à la biologie*.

Hüppop, O., & Hüppop, K. (2011). Bird migration on Helgoland : The yield from 100 years of research. *Journal of Ornithology*, *152*(S1), 25-40. https://doi.org/10.1007/s10336-011-0705-2

Inger, R., Harrison, X. A., Ruxton, G. D., Newton, J., Colhoun, K., Gudmundsson, G. A., McElwaine, G., Pickford, M., Hodgson, D., & Bearhop, S. (2010). Carry-over effects reveal reproductive costs in a long-distance migrant. *Journal of Animal Ecology*, *79*(5), 974-982. https://doi.org/10.1111/j.1365-2656.2010.01712.x

Jacobs, J. D., & Wingfield, J. C. (2000). Endocrine Control of Life-Cycle Stages : A Constraint on Response to the Environment? *The Condor*, *102*(1), 35-51. https://doi.org/10.2307/1370406

Jarjour, C., Frei, B., & Elliott, K. H. (2017). Associations between sex, age and species-specific climate sensitivity in migration. *Animal Migration*, *4*(1), 23-36. https://doi.org/10.1515/ami-2017-0004

Jenni, L., & Kéry, M. (2003). Timing of autumn bird migration under climate change : Advances in long–distance migrants, delays in short–distance migrants. *Proceedings of the Royal Society B: Biological Sciences*, *270*(1523), 1467-1471. https://doi.org/10.1098/rspb.2003.2394

Jenni, L., & Schaub, M. (2003). Behavioural and Physiological Reactions to Environmental Variation in Bird Migration : A Review. In P. Berthold, E. Gwinner, & E. Sonnenschein (Éds.), *Avian Migration* (p. 155-171). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-662-05957-9_10

Jia, R., Zhang, G., Wang, Y., Yang, Z., Xu, H., Sun, G., Ma, T., Gao, R., Ru, W., Ji, Z., & Li, D. (2024). Coeffects of temperature and photoperiod on the age-related timing of spring migration of Whooper swans via satellite tracking. *Global Ecology and Conservation*, *51*, e02895. https://doi.org/10.1016/j.gecco.2024.e02895

Kassara, C., Barboutis, C., & Bounas, A. (2025). Favorable stopover sites and fuel load dynamics of spring bird migrants under a changing climate. *Climatic Change*, *178*(1), 3. https://doi.org/10.1007/s10584-024-03829-9

Kayser, B. (2024). *Træktælling ved Gedser Fuglestation*.

King, D. T., Wang, G., & Cunningham, F. L. (2022). Large- and Small-Scale Climate Influences Spring Migration Departure Probability of American White Pelicans. *Diversity*, *14*(6). https://doi.org/10.3390/d14060500

Kingsolver, J. G., Higgins, J. K., & Augustine, K. E. (2015). Fluctuating temperatures and ectotherm growth : Distinguishing non-linear and time-dependent effects. *Journal of Experimental Biology*, *218*(14), 2218-2225. https://doi.org/10.1242/jeb.120733

Kjellén, N. (1992). Differential Timing of Autumn Migration between Sex and Age Groups in Raptors at Falsterbo, Sweden. *Ornis Scandinavica (Scandinavian Journal of Ornithology)*, *23*(4), 420-434. https://doi.org/10.2307/3676673

Klinges, D. H., Muñoz, M. M., Domínguez-Guerrero, S. F., Maclean, I. M. D., Kearney, M. R., & Skelly, D. K. (2026). Matching climate to biological scales. *Trends in Ecology & Evolution*, *41*(4). https://doi.org/10.1016/j.tree.2025.11.015

Klinner, T., Buddemeier, J., Bairlein, F., & Schmaljohann, H. (2020). Decision-making in migratory birds at stopover : An interplay of energy stores and feeding conditions. *Behavioral Ecology and Sociobiology*, *74*(1), 10. https://doi.org/10.1007/s00265-019-2784-7

Kokko, H. (1999). Competition for early arrival in migratory birds. *Journal of Animal Ecology*, *68*(5), 940-950. https://doi.org/10.1046/j.1365-2656.1999.00343.x

Larsson, K., Hajdu, S., Kilpi, M., Larsson, R., Leito, A., & Lyngs, P. (2014). Effects of an extensive *Prymnesium polylepis* bloom on breeding Eiders in the Baltic Sea. *Journal of Sea Research*, *88*, 21-28. https://doi.org/10.1016/j.seares.2013.12.017

Laursen, K. (1989). Estimates of Sea Duck Winter Populations of the Western Palaearctic. *Danish Revue of Game Biology*, *13*(6).

Laursen, K., Møller, A. P., & Hobson, K. (2019). N-Isotopes in Feathers and Abundance of Eiders Respond to Nutrients in Seawater. *Ecosystems*, *22*, 1271-1279. https://doi.org/10.1007/s10021-018-00334-w

Leyrer, J., Pruiksma, S., & Piersma, T. (2011). On 4 June 2008 Siberian Red Knots at Elbe Mouth Kissed the Canonical Evening Migration Departure Rule Goodbye. *Ardea*, *97*, 71-79. https://doi.org/10.5253/078.097.0109

Liechti, F. (2006). Birds : Blowin' by the wind? *Journal of Ornithology*, *147*(2), 202-211. https://doi.org/10.1007/s10336-006-0061-9

Lind, H. (2010). *Fuglestationens historie*. Gedser Fuglestation. https://www.gedserfuglestation.dk/om-fuglestationen/fuglestationens-historie

Lindberg, M. S., & Walker, J. (2007). Satellite Telemetry in Avian Research and Management : Sample Size Considerations. *The Journal of Wildlife Management*, *71*(3), 1002-1009. https://doi.org/10.2193/2005-696

Liu, M., & Swanson, D. (2015). Stopover duration, movement patterns and temporary home ranges of fall migrant Yellow-rumped Warblers (*Setophaga coronata*) in native and anthropogenic woodlands of the Northern Prairie region, USA. *Journal of Avian Biology*, *46*(5), 452-461. https://doi.org/10.1111/jav.00672

Lüdecke, D., Ben-Shachar, M. S., Patil, I., Waggoner, P., & Makowski, D. (2021). performance : An R Package for Assessment, Comparison and Testing of Statistical Models. *Journal of Open Source Software*, *6*(60), 3139. https://doi.org/10.21105/joss.03139

Martín, B., Onrubia, A., de la Cruz, A., & Ferrer, M. (2016). Trends of autumn counts at Iberian migration bottlenecks as a tool for monitoring continental populations of soaring birds in Europe. *Biodiversity and Conservation*, *25*(2), 295-309. https://doi.org/10.1007/s10531-016-1047-4

Masden, E. A., Haydon, D. T., Fox, A. D., Furness, R. W., Bullman, R., & Desholm, M. (2009). Barriers to movement : Impacts of wind farms on migrating birds. *ICES Journal of Marine Science*, *66*(4), 746-753. https://doi.org/10.1093/icesjms/fsp031

Mayor, S. J., Guralnick, R. P., Tingley, M. W., Otegui, J., Withey, J. C., Elmendorf, S. C., Andrew, M. E., Leyk, S., Pearse, I. S., & Schneider, D. C. (2017). Increasing phenological asynchrony between spring green-up and arrival of migratory birds. *Scientific Reports*, *7*(1), 1902. https://doi.org/10.1038/s41598-017-02045-z

Miller, R. A., Onrubia, A., Martín, B., Kaltenecker, G. S., Carlisle, J. D., Bechard, M. J., & Ferrer, M. (2016). Local and regional weather patterns influencing post-breeding migration counts of soaring birds at the Strait of Gibraltar, Spain. *Ibis*, *158*(1), 106-115. https://doi.org/10.1111/ibi.12326

Morales-Góngora, Y., Negrete-Yankelevich, S., Fox, G. A., Gallinat, A. S., Gallina-Tessaro, S., Goodrich, L. J., Hoffman, S. W., & Ruelas Inzunza, E. (2025). How much can local weather conditions explain intra- and inter-annual variation in raptor migration counts at a Neotropical hotspot? A new analytical approach. *Ornithology*, ukaf071. https://doi.org/10.1093/ornithology/ukaf071

Morelli, F., Laursen, K., Svitok, M., Benedetti, Y., & Moller, A. (2021). Eiders, nutrients and eagles : Bottom-up and top-down population dynamics in a marine bird. *Journal of Animal Ecology*, *90*, 1844-1853. https://doi.org/10.1111/1365-2656.13498

Mosbech, A., Gilchrist, G., Merkel, F., Sonne, C., Flagstad, A., & Nyegaard, H. (2006). Year-round movements of Northern Common Eiders *Somateria mollissima borealis* breeding in Arctic Canada and West Greenland followed by satellite telemetry. *Ardea*, *94*(3), 651-665.

Newton, I. (2008). *The Migration Ecology of Birds*. Academic Press. https://doi.org/10.1016/B978-0-12-517367-4.X5000-1

Newton, I. (2025). Migration mortality in birds. *Ibis*, *167*(1), 106-123. https://doi.org/10.1111/ibi.13316

Norris, D. R. (2005). Carry-Over Effects and Habitat Quality in Migratory Populations. *Oikos*, *109*(1), 178-186.

O'Neal, B. J., Stafford, J. D., Larkin, R. P., & Michel, E. S. (2018). The effect of weather on the decision to migrate from stopover sites by autumn-migrating ducks. *Movement Ecology*, *6*(1), 23. https://doi.org/10.1186/s40462-018-0141-5

Ożarowska, A., & Meissner, W. (2024). Increasing body condition of autumn migrating Eurasian blackcaps *Sylvia atricapilla* over four decades. *The European Zoological Journal*, *91*(1), 151-161. https://doi.org/10.1080/24750263.2024.2304735

Panuccio, M., Martín, B., Morganti, M., Onrubia, A., & Ferrer, M. (2017). Long-term changes in autumn migration dates at the Strait of Gibraltar reflect population trends of soaring birds. *Ibis*, *159*(1), 55-65. https://doi.org/10.1111/ibi.12420

QGIS.org, 2026. QGIS Geographic Information System. QGIS Association. http://www.qgis.org

R Core Team. (2025). _*R: A Language and Environment for Statistical Computing*_ (Version 4.5.2) [Logiciel]. R Foundation for Statistical Computing. https://www.R-project.org/

Ramenofsky, M. (2011). Hormones in Migration and Reproductive Cycles of Birds. In *Hormones and Reproduction of Vertebrates—Volume 4* (p. 205-237). https://doi.org/10.1016/B978-0-12-374932-1.00046-9

Richardson, W. J. (1978). Timing and Amount of Bird Migration in Relation to Weather : A Review. *Oikos*, *30*(2), 224-272. https://doi.org/10.2307/3543482

Robertson, A. M., Piggott, J. J., & Penk, M. R. (2024). Improving multiple stressor-response models through the inclusion of nonlinearity and interactions among stressor gradients. *Environmental Monitoring and Assessment*, *196*(11), 1026. https://doi.org/10.1007/s10661-024-13169-x

Rüppel, G., Hüppop, O., Lagerveld, S., Schmaljohann, H., & Brust, V. (2023). Departure, routing and landing decisions of long-distance migratory songbirds in relation to weather. *Royal Society Open Science*, *10*(2), 221420. https://doi.org/10.1098/rsos.221420

Salomonsen, F. (1968). The moult migration. *Wildfowl*, *19*, 5-24.

Schaub, M., Liechti, F., & Jenni, L. (2004). Departure of migrating European robins, *Erithacus rubecula*, from a stopover site in relation to wind and rain. *Animal Behaviour*, *67*(2), 229-237. https://doi.org/10.1016/j.anbehav.2003.03.011

Schmaljohann, H., Lisovski, S., & Bairlein, F. (2017). Flexible reaction norms to environmental variables along the migration route and the significance of stopover duration for total speed of migration in a songbird migrant. *Frontiers in Zoology*, *14*(1), 17. https://doi.org/10.1186/s12983-017-0203-3

Seinfeld, J. H., & Pandis, S. N. (2016). *Atmospheric Chemistry and Physics : From Air Pollution to Climate Change*. John Wiley & Sons.

Senner, N. R., Stager, M., Verhoeven, M. A., Cheviron, Z. A., Piersma, T., & Bouten, W. (2018). High-altitude shorebird migration in the absence of topographical barriers : Avoiding high air temperatures and searching for profitable winds. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1881), 20180569. https://doi.org/10.1098/rspb.2018.0569

Sergio, F., Tanferna, A., Stephanis, R., Lopez-Jimenez, L., Blas, J., Tavecchia, G., Preatoni, D., & Hiraldo, F. (2014). Individual improvements and selective mortality shape lifelong migratory performance. *Nature*, *515*, 410-413. https://doi.org/10.1038/nature13696

Shamoun-Baranes, J., Bouten, W., & van Loon, E. E. (2010). Integrating Meteorology into Research on Migration. *Integrative and Comparative Biology*, *50*(3), 280-292. https://doi.org/10.1093/icb/icq011

Shamoun-Baranes, J., Liechti, F., & Vansteelant, W. M. G. (2017). Atmospheric conditions create freeways, detours and tailbacks for migrating birds. *Journal of Comparative Physiology A*, *203*(6-7), 509-529. https://doi.org/10.1007/s00359-017-1181-9

Shamoun-Baranes, J., Van Loon, E., Alon, D., Alpert, P., Yom-Tov, Y., & Leshem, Y. (2006). Is there a connection between weather at departure sites, onset of migration and timing of soaring-bird autumn migration in Israel? *Global Ecology and Biogeography*, *15*(6), 541-552. https://doi.org/10.1111/j.1466-8238.2006.00261.x

SMHI. (2026). *Ladda ner väderobservationer*. SMHI. https://www.smhi.se/data/hitta-data-for-en-plats/ladda-ner-vaderobservationer

Tjørnløv, R. S., Pradel, R., Choquet, R., Christensen, T. K., & Frederiksen, M. (2019). Consequences of past and present harvest management in a declining flyway population of common Eiders *Somateria mollissima* . *Ecology and Evolution*, *9*(22), 12515-12530. https://doi.org/10.1002/ece3.5707

Trektellen. (2026a). *Eiders migration map (1970—2026)*. Trektellen. https://www.trektellen.org/maps/species/-6/0/73/19700101/20260827/0/0

Trektellen. (2026b). *Gedser Bird Observatory*. Trektellen. https://www.trektellen.org/site/info/1334

Tsvey, A., Bulyuk, V. N., & Kosarev, V. (2007). Influence of body condition and weather on departures of first-year European robins *Erithacus rubecula* from an autumn migratory stopover site. *Behavioral Ecology and Sociobiology*, *61*(11), 1665-1674. https://doi.org/10.1007/s00265-007-0397-z

Underhill, L. G., & Remisiewicz, M. (2025). Arrival and Peak Abundance of Barn Swallows *Hirundo rustica* in Three Regions of South Africa in Relation to Climate Indices, Deduced from Bird Atlas Data. *Birds*, *6*(48). https://doi.org/https://doi.org/10.3390/ birds6030048

Van De Pol, M., Bailey, L. D., McLean, N., Rijsdijk, L., Lawson, C. R., & Brouwer, L. (2016). Identifying the best climatic predictors in ecology and evolution. *Methods in Ecology and Evolution*, *7*(10), 1246-1257. https://doi.org/10.1111/2041-210X.12590

Vanausdall, R. A., Kendall, W. L., Collins, D. P., & Hays, Q. R. (2024). Time of year and weather influence departure decisions of sandhill cranes at a primary stopover. *Frontiers in Ecology and Evolution*, *12*, 1279279. https://doi.org/10.3389/FEVO.2024.1279279

Vansteelant, W. M. G., Verhelst, B., Shamoun-Baranes, J., Bouten, W., Van Loon, E. E., & Bildstein, K. L. (2014). Effect of wind, thermal convection, and variation in flight strategies on the daily rhythm and flight paths of migrating raptors at Georgia's Black Sea coast : Migrating Raptors at Georgia's Black Sea Coast. *Journal of Field Ornithology*, *85*(1), 40-55. https://doi.org/10.1111/jofo.12048

Visser, M. E., & Both, C. (2005). Shifts in phenology due to global climate change : The need for a yardstick. *Proceedings of the Royal Society B: Biological Sciences*, *272*(1581), 2561-2569. https://doi.org/10.1098/rspb.2005.3356

Weber, T. P., Alerstam, T., & Hedenström, A. (1998). Stopover Decisions under Wind Influence. *Journal of Avian Biology*, *29*, 552-560. https://doi.org/10.2307/3677175

Weber, T. P., Fransson, T., & Houston, A. I. (1999). Should I stay or should I go? Testing optimality models of stopover decisions in migrating birds. *Behavioral Ecology and Sociobiology*, *46*(4), 280-286. https://doi.org/10.1007/s002650050621

Wehrmann, J., de Boer, F., Benjumea, R., Cavaillès, S., Engelen, D., Jansen, J., Verhelst, B., & M.G. Vansteelant, W. (2019). Batumi Raptor Count : Autumn raptor migration count data from the Batumi bottleneck, Republic of Georgia. *ZooKeys*, *836*, 135-157. https://doi.org/10.3897/zookeys.836.29252

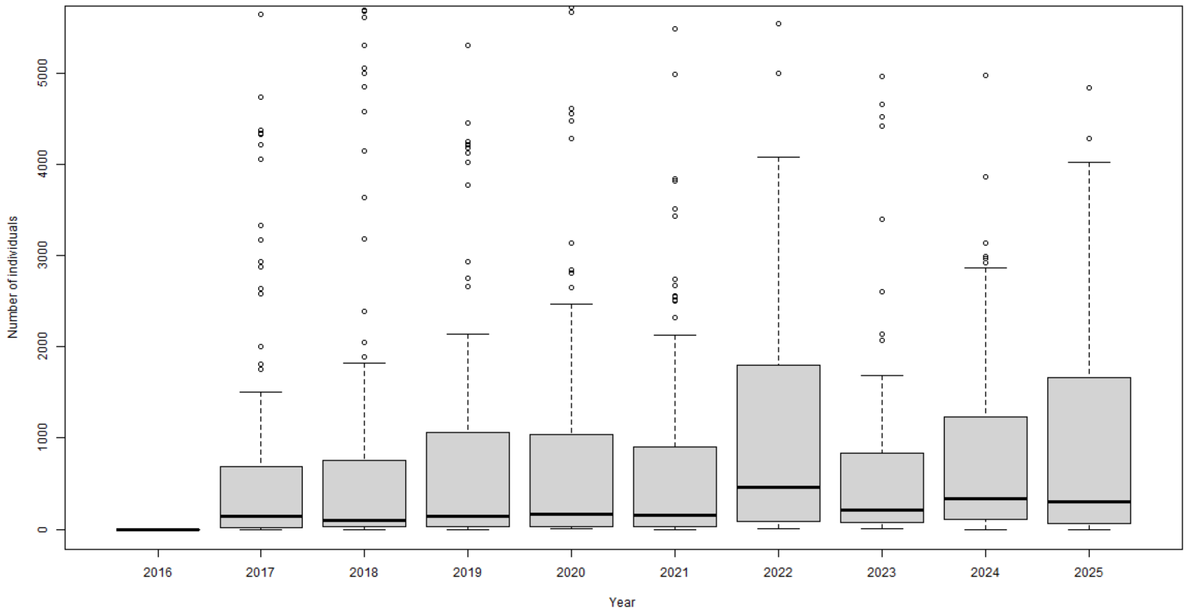
Werfeli, M., Ranacher, P., & Liechti, F. (2022). Gone with the wind : Inferring bird migration with light-level geolocation, wind and activity measurements. *Methods in Ecology and Evolution*, *13*(6), 1265-1274. https://doi.org/10.1111/2041-210X.13837

Winger, B. M., La Sorte, F. A., Hack, M. D., & Pegan, T. M. (2025). Joint evolution of the biogeography and phenology of seasonal migration. *PNAS Nexus*, *4*(8), pgaf247. https://doi.org/10.1093/pnasnexus/pgaf247

Xu, F., & Si, Y. (2019). The frost wave hypothesis : How the environment drives autumn departure of migratory waterfowl. *Ecological Indicators*, *101*, 1018-1025. https://doi.org/10.1016/j.ecolind.2019.02.024

SUPPLEMENTARY MATERIALS

S1 : Boxplot of the yearly number of Eiders. Median is shown in black and whiskers displays 25% and 75 quantiles. In order to help visualization, the upper limit of the y-axis was set to 95% quantile of the whole dataset (range [0;32325]).



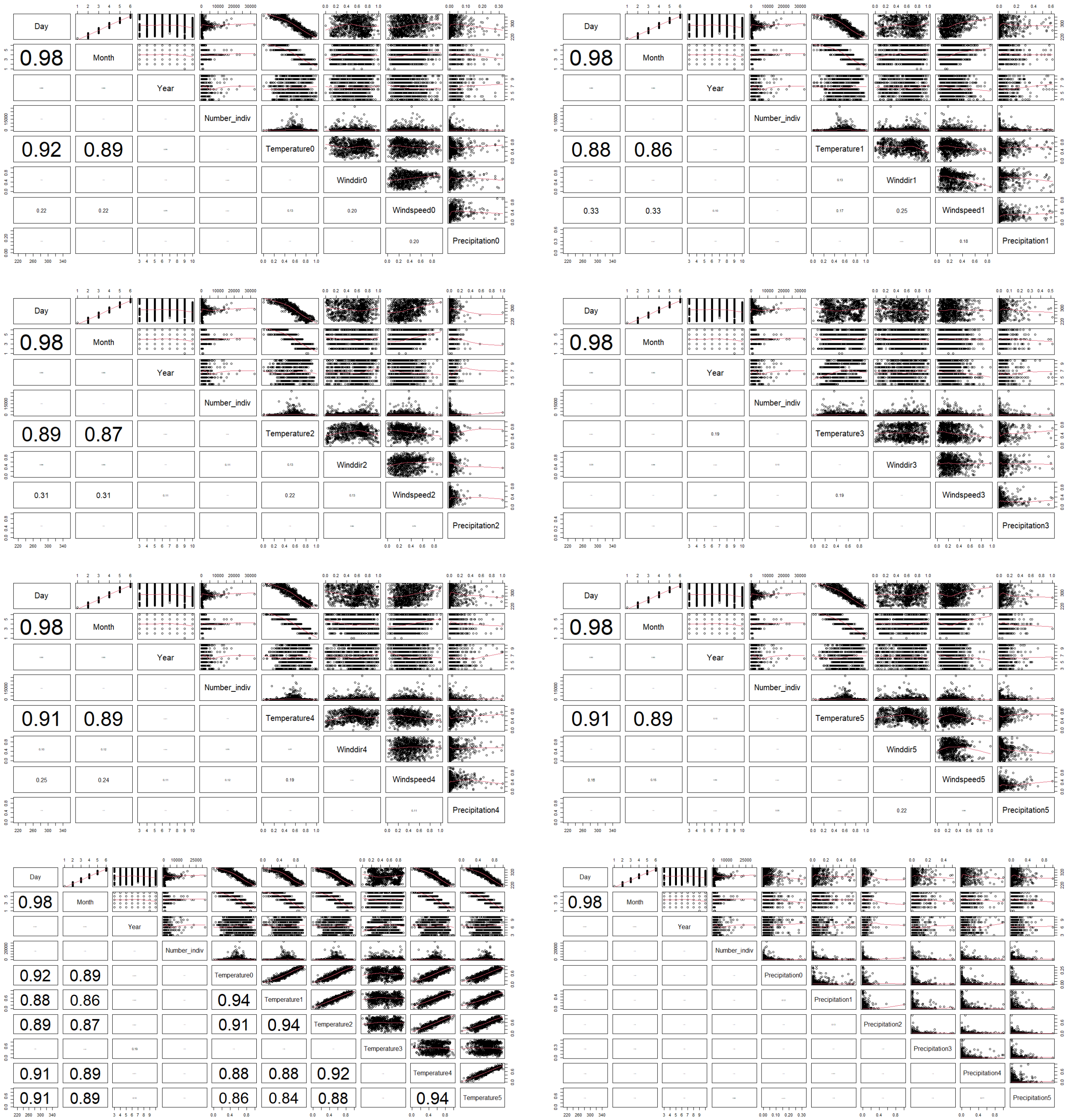
S2 : Complementary analysis regarding wind in Skillinge. Marginal means estimated from a Linear Model (Gaussian distribution) "Wind speed ~ Wind direction" measured in Skillinge only (χ^2 = 134.98 ; *p* = 2.2e-16). The Estimated Marginal Mean (EMMean) is pictured with standard error (SE), confidence interval (lower and upper CL). Significant differences in wind speed between directions is depicted by the Group to which they have been assigned.

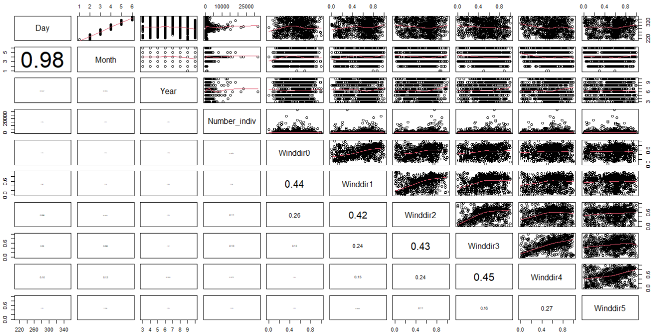
Wind Direction	EMMean	SE	lower CL	upper CL	Group
North	4.69	0.454	3.79	5.58	C
NE	5.18	0.209	4.77	5.59	B
East	6.07	0.215	5.64	6.49	A
SE	4.57	0.236	4.10	5.03	B
South	4.36	0.188	3.99	4.73	B
SW	4.85	0.126	4.61	5.10	B
West	3.94	0.136	3.68	4.21	B
NW	2.81	0.248	2.32	3.29	B

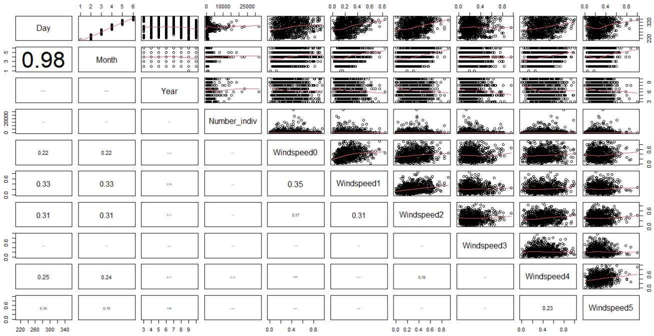
S3 : Full model comparison table. Intercept, estimates for each included variable, Akaike's criterion (AIC), the difference in Akaike's criterion compared with the best model (ΔAIC), Akaike's weight (w), R2 conditional and R2 marginal characterising each model. Estimates are shown in bold when the variable has a significant effect (p-value < 0.05). Variables shown in red are never significant, regardless of the models in which they are included, whilst variables shown in green have a significant effect in all models in which they are included. Lowest AIC and highest R2 conditional are shown in bold.

		Local					1 day lagged					2 days lagged					3 days lagged					4 days lagged					5 days lagged									
Model name	(Intercept)	Temperature0	Winddir0	Windspeed0	Precipitation0	Winddir0: Windspeed0	Temperature1	Winddir1	Windspeed1	Precipitation1	Winddir1: Windspeed1	Temperature2	Winddir2	Windspeed2	Precipitation2	Winddir2: Windspeed2	Temperature3	Winddir3	Windspeed3	Precipitation3	Winddir3: Windspeed3	Temperature4	Winddir4	Windspeed4	Precipitation4	Winddir4: Windspeed4	Temperature5	Winddir5	Windspeed5	Precipitation5	Winddir5: Windspeed5	AIC	Δ AIC	AIC weight	R2 conditional	R2 marginal
Local+Lag	6,043	0,633	**-0,568**	1,914	**-5,566**	**-3,413**	-1,184	-0,158	**1,021**	-0,224	-0,199		**0,824**	0,438	0,681	-0,794	**0,647**	-0,179	-0,336	0,284	0,890		**0,146**	-0,185	-0,381	0,959		-0,503	-0,219	0,438	0,752	**14 332,616**	0,000	1,000E+00	**0,619**	0,102
Local1234	5,831	0,745	**-0,578**	1,837	**-5,483**	**-3,333**	-1,171	-0,146	**1,019**	-0,198	-0,125		**0,752**	0,321	0,660	-0,711	**0,642**	-0,104	-0,223	0,197	0,597		**0,046**	-0,221	-0,297	1,153						14 359,426	26,810	1,508E-06	0,616	0,095
Lag_only	5,149						-0,373	**-0,067**	2,111	-1,015	**-3,222**		**0,985**	1,004	0,946	-1,555	**0,724**	0,181	0,165	0,320	-0,372		**0,140**	-0,394	-0,176	1,104		-0,106	0,420	0,733	-0,246	14 380,971	48,354	3,162E-11	0,585	0,051
Lag1234	5,266						-0,364	**-0,081**	2,128	-1,038	**-3,099**		**0,906**	0,805	0,915	-1,407	**0,728**	0,265	0,240	0,253	-0,634		**0,005**	-0,412	-0,129	1,368						14 408,524	75,908	3,287E-17	0,584	0,047
Lag2345	5,342											-0,596	0,756	1,476	0,768	**-2,385**	**0,746**	0,211	0,467	0,459	-0,948		**0,005**	-0,510	-0,239	1,391		-0,055	0,574	0,901	0,117	14 503,106	170,489	9,522E-38	0,581	0,042
Lag234	5,547											-0,574	0,653	1,262	0,780	-2,162	**0,742**	0,290	0,499	0,332	-1,137		**-0,093**	-0,464	-0,227	1,686						14 533,079	200,463	2,952E-44	0,579	0,034
Local123	5,755	0,582	**-0,574**	1,975	**-5,480**	**-3,443**	-1,120	-0,101	**1,114**	-0,093	-0,383		**0,809**	0,347	0,495	-0,623	**0,704**	0,278	-0,156	0,150	0,326											14 613,577	280,960	9,779E-62	0,612	0,093
Lag123	5,181						-0,459	**-0,058**	2,247	-0,914	**-3,316**		**0,958**	0,805	0,777	-1,258	**0,771**	0,621	0,220	0,216	-0,719											14 664,962	332,346	6,793E-73	0,580	0,044
Lag23	5,483											-0,770	0,698	1,320	0,667	-2,011	**0,783**	0,705	0,576	0,249	-1,392											14 792,119	459,503	1,660E-100	0,575	0,029
Lag345	6,006																**0,728**	0,107	0,193	0,643	-0,485	-0,709	**-0,014**	-0,448	-0,218	1,346		-0,139	0,305	0,956	0,470	14 890,009	557,392	9,200E-122	0,585	0,040
Lag34	6,050																**0,720**	0,168	0,241	0,527	-0,674	-0,670	**-0,071**	**-0,396**	-0,205	1,570						14 919,197	586,580	4,224E-128	0,582	0,034
Local12	6,411	0,162	**-0,461**	2,157	**-5,627**	**-3,972**	-1,011	-0,355	**0,756**	-0,509	1,373		**0,872**	0,085	0,504	0,047																15 025,234	692,618	3,981E-151	0,613	0,100
Lag12	5,976						-0,683	**-0,262**	**2,076**	**-1,278**	-2,057		**1,008**	0,483	0,723	-0,473																15 082,104	749,488	1,781E-163	0,571	0,040
Lag3	5,547																**0,768**	**0,632**	0,228	0,367	-0,871											15 179,255	846,638	1,428E-184	0,580	0,019
Lag45	6,578																					-0,875	**-0,138**	-0,593	-0,308	1,795		-0,264	**0,392**	0,766	0,815	15 188,916	856,300	1,140E-186	0,583	0,041
Lag4	6,623																					-0,851	**-0,190**	**-0,533**	-0,292	**2,078**						15 220,693	888,076	1,434E-193	0,578	0,032
Local1	6,877	0,374	**-0,405**	2,147	**-5,695**	**-3,869**	-1,336	-0,241	**-0,027**	-0,419	**2,920**																					15 433,766	1 101,150	7,734E-240	0,614	0,087
Lag2	6,495											**-1,218**	0,598	0,904	0,497	-0,855																15 468,235	1 135,619	2,532E-247	0,567	0,029
Lag1	6,750						-0,972	-0,225	**1,092**	**-1,159**	-0,119																					15 488,274	1 155,658	1,127E-251	0,575	0,029
Lag5	6,468																										-0,785	-0,190	**0,798**	**0,993**	0,846	15 820,949	1 488,332	4,941E-324	0,574	0,027
Local_only	6,247	0,110	**-0,281**	2,262	-0,904	**-3,623**																										15 824,116	1 491,499	0,000E+00	0,588	0,041

S4 : Pairplots of the factors included for each lag (Local to 5-day lag) and of the weather parameters. Names of the factors are in the diagonal of each matrix. The upper panels show scatterplots with the global pattern in red, and the lower panels contain the Pearson correlation coefficients. The font of the correlation coefficient is proportional to its estimated value.




Day
0.98
Month
Year
Number_indiv
Winddir0
0.44
Winddir1
0.26
0.42
Winddir2
0.24
0.43
Winddir3
0.24
0.45
Winddir4
0.27
Winddir5


Day
0.98
Month
Year
Number_indiv
0.22
0.22
Windspeed0
0.33
0.33
0.35
Windspeed1
0.31
0.31
0.31
Windspeed2
Windspeed3
0.25
0.24
Windspeed4
0.23
Windspeed5